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A Revision of the Chelonian Genus Bothremys (Pleurodira: Pelomedusidae)

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ACKNOWLEDGEMENTS

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INTRODUCTION

In the fall of 1945 the late C. M. Barber with the help of Karl P. Schmidt, then Chief Curator of Zoology, and I instigated a program

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of collecting vertebrates in the Mooreville Chalk of Alabama. By 1948 most localities had been thoroughly searched and most of them had been revisited a number of times, but Mr. Barber proposed one last trip in the fall of 1949 for which he and I received a grant from the Geological Society of America (No. 661-55). This is herewith gratefully acknowledged.

It was on this occasion that Mr. Barber, accompanied by Mr. J. A. Robbins, collected a most significant specimen, a virtually complete shell of the pelomedusine *Podocnemis alabamae* associated with a partial skull and a mandible (FMNH PR 247). This mandible clearly showed that the material heretofore assigned to *Podocnemis alabamae* properly belongs to the genus *Bothremys* Leidy.

While visiting collections of East Coast Institutions in connection with my study of the protostegid and toxochelyid turtles of this fauna, I discovered in the Peabody collection, Yale University, a tray full of turtle shell fragments from the Niobrara Chalk of Kansas, and recognized them as belonging to a pelomedusine closely allied to the Alabama and Arkansas forms. The specimen has since been piece-fitted, and is described below.

In casual conversation with Dr. Horace Richards of the Philadelphia Academy of Sciences, I suggested that the turtles of the New Jersey Greensand probably occur often in whole shells, and that the fragmentary condition of most of the material from New Jersey is due to casual collecting. Dr. Richards instructed interested young collectors, Albert Jehle and Henry B. Roberts, in the proper collection of fossil material in the Greensand pits and this brought forth striking results. Within a few months, the bony plates of a large turtle arrived at Field Museum and these could easily be piece-fitted to form a nearly complete shell. This find also belongs to a pelomedusine closely related to the Alabama and Arkansas forms. The revisions made necessary by these materials are in the present paper.

RAINER ZANGERL

EMENDED DIAGNOSIS

Order Chelonia

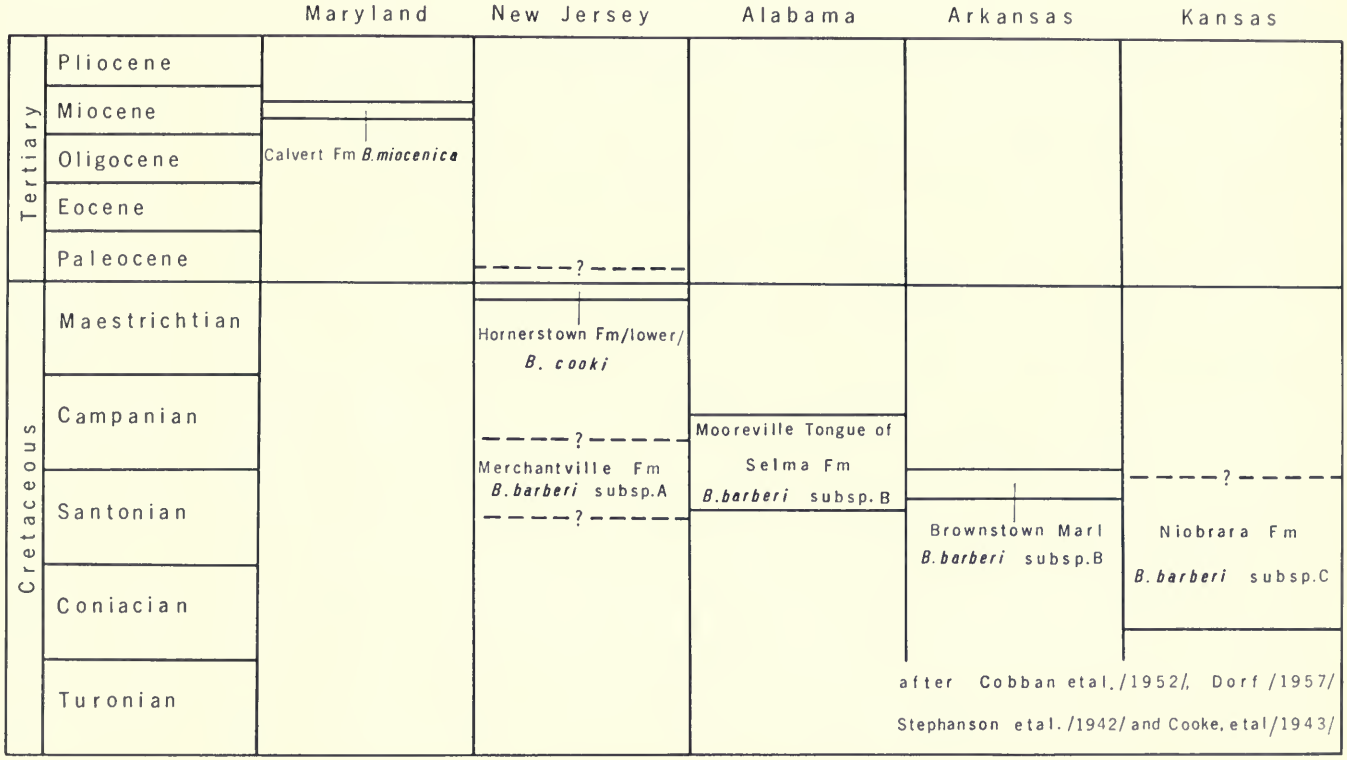
Suborder Pleurodira

Family Pelomedusidae

Genus *Bothremys* Leidy, 1865

FIG. 1. Correlation chart.

Distribution of the genus Bothremys.



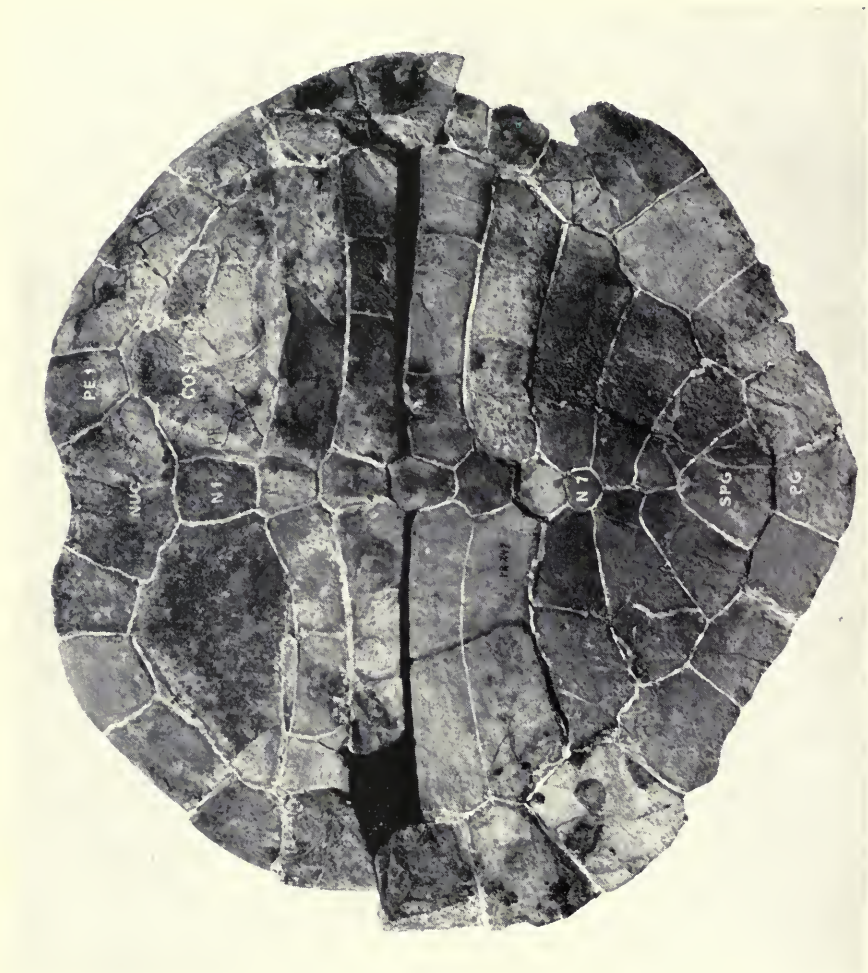


FIG. 2. *Bothremys barberi*, spp. B (FMNH PR 247), Selma Formation, Alabama, dorsal view of carapace. Shell is flattened and distorted, the width is greater than it was in life. N - neural, NUC - nuchal, PE - peripheral, COST - costal, PG - pygal, SPG - suprapygal.

Type species: Bothremys cooki

Skull wide and flat, orbits facing dorsad. Palate dominated by large pits in the center of wide triturating surfaces. Pits formed by jugals widely exposed on triturating surfaces. Well developed vomer separating internal nares. *Processus pterygoideus externus* as in living pelomedusids. Quadrate closed behind stapedial opening.

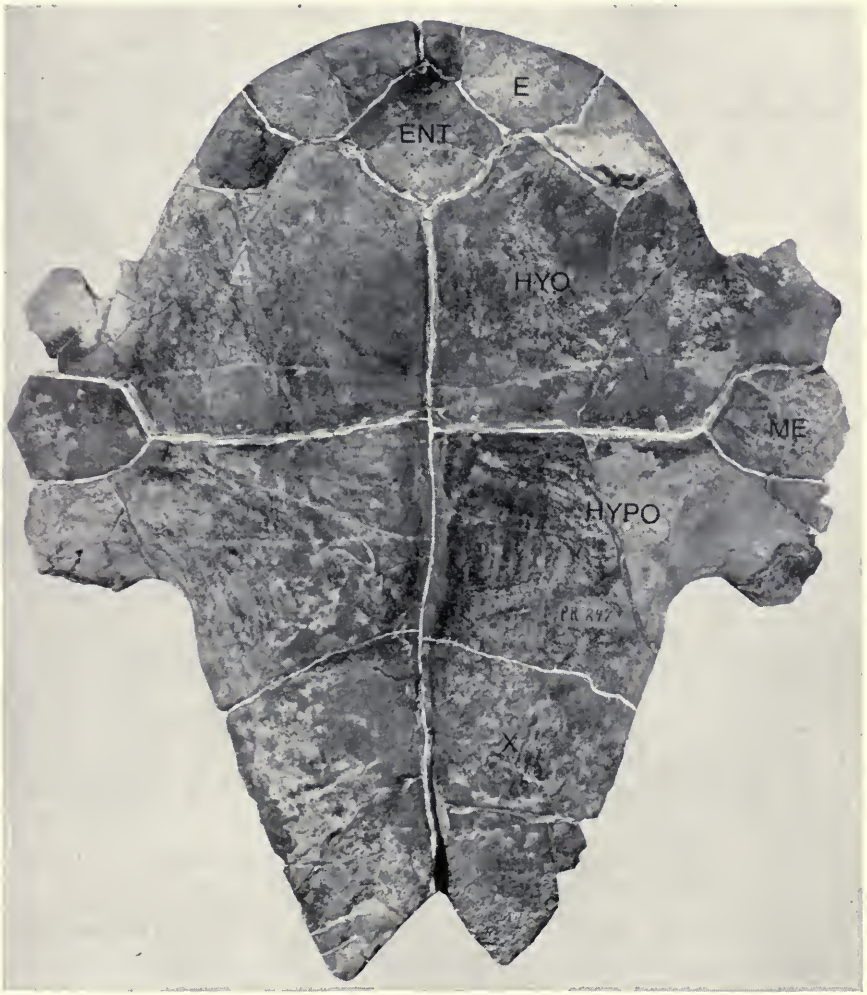


FIG. 3. *Bothremys barberi*, spp. B (FMNH PR 247), Selma Formation, Alabama, ventral view of plastron. E - epiplastron, ENT - entoplastron, HYO -hyoplastron, HYPO - hypoplastron, ME - mesoplastron, X - xiphiplastron. Sagittal length is 48.5 cm.

Probable contact of quadrate with basisphenoid. *Processus articularis* on same vertical plane with *condylus occipitalis*. No enlarged carotid opening.

Known appendicular elements similar to *Podocnemis expansa*. Carapace oval, moderately arched. Nuchal hexagonal, broader posteriorly, anterior edge notched. Neurals vary from six to seven.

Costals 2 - 4 tend to be much shorter in relation to their width as in *Taphrosphys*, but as opposed to *Podocnemis*. Eleven peripherals, free edges mostly acute but varying to obtuse in large individuals. No cervical scute, pleural scales extending onto peripherals. Anterior lobe of plastron short, broad, and rounded. Posterior lobe long, tapering posteriorly. Xiphiplastral notch broad and U-shaped, xiphiplastra end in rounded projections. Large, quadrilateral entoplastron. Mesoplastra small and well onto bridge. Pubic scar short and wide, ischiac scar triangular and away from xiphiplastral edge. Intergular V-shaped and separating small gulars and part of humerals.

The species cannot be diagnosed at this time.

DISCUSSION OF SPECIES

Bothremys cooki Leidy, 1865

A skull and mandible (Figs. 13, 14, 15, 16, 22) are the only known specimens of this species. It was found in 1862, described by Leidy in 1865 (pp. 110-113), and re-examined by Hay in 1908 (pp. 103-104). The original locality data (Leidy, 1865, p. 110) reads: "the Green-sand near Barnsboro, Gloucester County, New Jersey." The skull's age was presumed to be Late Cretaceous, but subsequent revisions of New Jersey stratigraphy show that the age could be either Late Cretaceous or Lower Tertiary (see Miller, 1956; Olsson, 1963; and Baird, 1964). However, the most prolific vertebrate horizons in this area are the lowermost Hornerstown Formation and the Navesink Formation, both of which are Maestrichtian.

Even though the jaws of *B. cooki* and *B. barberi* (see below) are very similar, the authors think it best to retain the species distinction until associated shell material becomes available for *B. cooki*.

Bothremys barberi (Schmidt)

Podocnemis barberi Schmidt, 1940

Podocnemis alabamae Zangerl, 1948

The discovery of a lower jaw (Fig. 22) almost identical to *Bothremys cooki* associated with a nearly complete carapace and plastron (Figs. 2, 3) of *"Podocnemis alabamae"* has made it necessary to change the generic assignment of *"P. alabamae."* The differences between *"P. barberi"* and *"P. alabamae"*seem trivial in the light of material from New Jersey and Kansas; we thus believe that these two forms

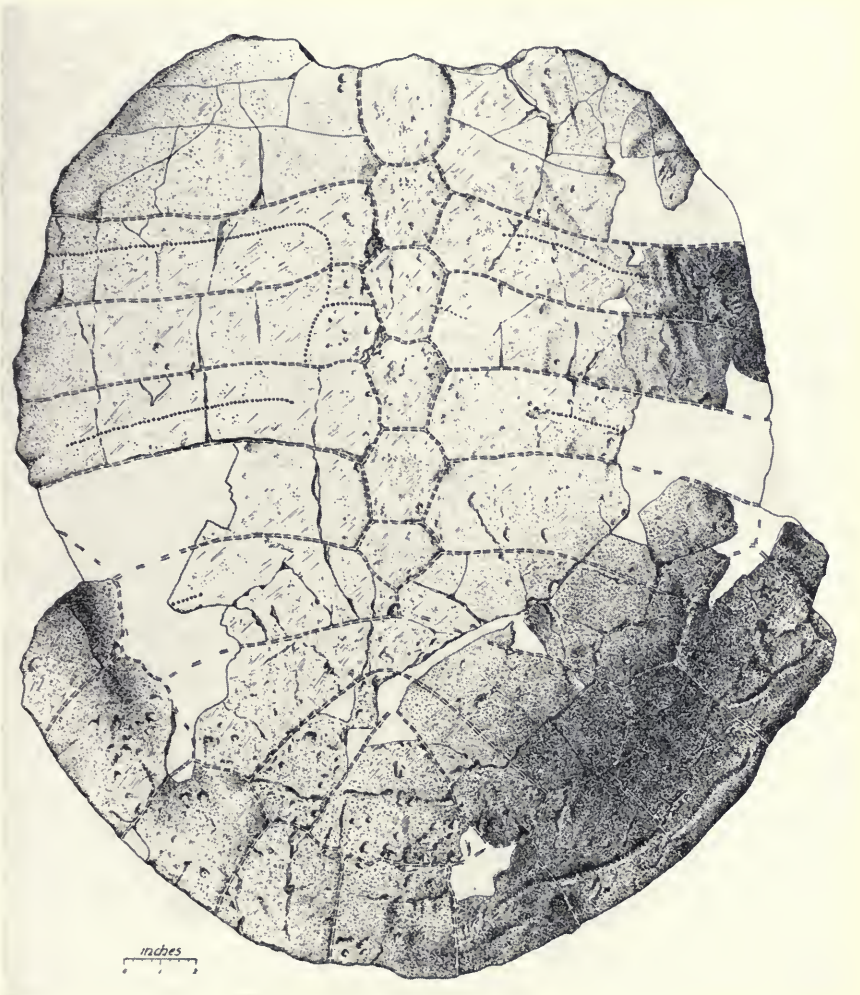


FIG. 4. *Bothremys barberi*, spp. A (ANSP 15902), Merchantville Formation, New Jersey, dorsal view of carapace.

are conspecific. "*P. alabamae*" becomes a synonym of "*P. barberi*," as the oldest available name for this species.

The generic re-assignment is based on a weathered but almost entirely complete specimen (Figs. 2, 3) collected by Mr. C. M. Barber in the Mooreville Tongue of the Selma Formation, one mile east of Harrell, Dallas Co., Alabama (FMNH PR 247). The shell is readily identified as "*Podocnemis alabamae*." The associated skull ma-

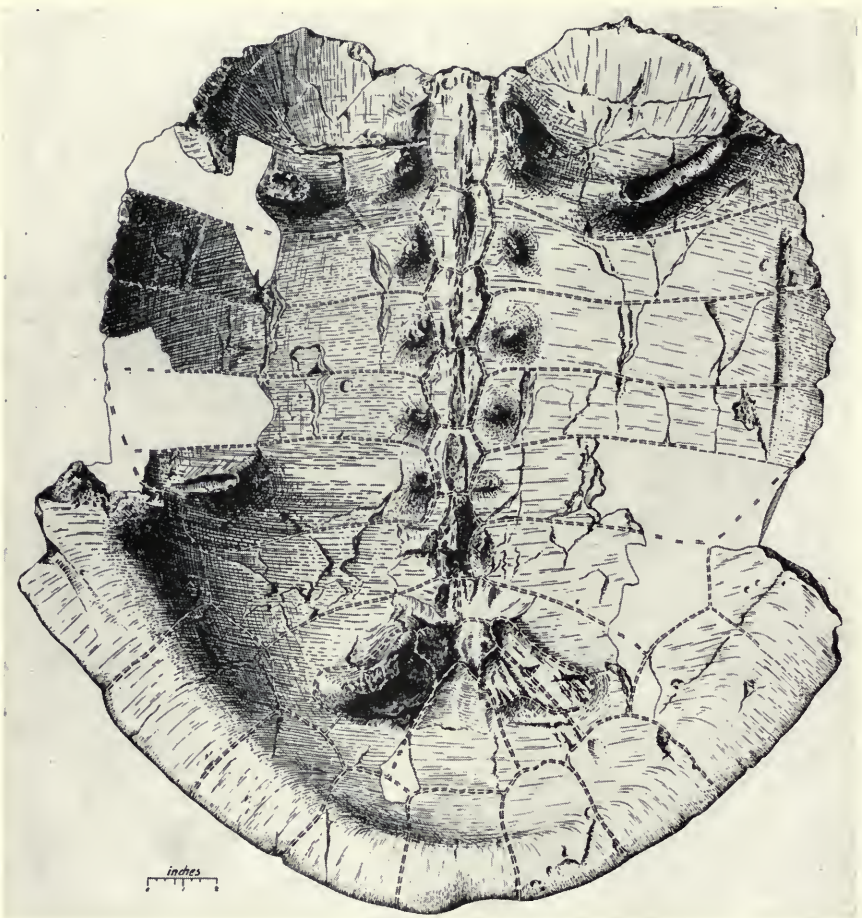


FIG. 5. *Bothremys barberi*, spp. A (ANSP 15902), Merchantville Formation, New Jersey, ventral view of carapace.

terial consists of a complete lower jaw, water-worn around the edge, plus portions of the brain case and right otic capsule described below. Comparison of *B. barberi's* jaw with the type of *Bothremys cooki* reveals no important differences.

As can be seen from the correlation chart (Fig. 1) there are a number of specimens of *B. barberi* occurring in formations of about the same stratigraphic horizon from New Jersey to Kansas. This suggests the possibility of subspecies along the Cretaceous coastline. Such an arrangement would be feasible in view of subspecific differentiation of modern turtles along the Gulf Coastal Plain (*e. g.*,

Graptemys, where virtually every major river has its distinct subspecies). In the case of the Cretaceous coastline, it seems not too unreasonable to distinguish Atlantic, Gulf, and epicontinental coastal provinces, especially since the Gulf province was deeply indented by the Mississippi embayment. In view of what is known of subspeciation in modern turtles, it is likely that if large enough samples were available, these three groups could be defined statistically. However, since two of the samples (New Jersey and Kansas) consist only of one specimen each, it is impossible to differentiate between variation on a population level and individual variation. As a compromise between theoretical considerations and the practical limits of the material, we propose to designate these subspecies by letters but not name them formally.

Subspecies A: The Atlantic Coastal Province

A nearly complete shell from New Jersey (ANSP 15902, Figs. 4–8) extends the geographic range of the species to the East Coast. The specimen was found in the Merchantville Formation at Graham Brick Yards, Maple Shade, New Jersey, in 1945, by Albert Jehle and Henry B. Roberts (Dr. Horace Richards, personal communication). The Merchantville Formation consists of "black, glauconitic, micaceous clay with occasional sand layers" (Dorf, 1957, p. 192) and is believed to be lower Campanian in age (*ibid.*) or upper Santonian (Stephenson *et al.*, 1942). In addition to this specimen, the known vertebrate fauna of the Merchantville (Miller, 1955, p. 904) includes fish teeth, mosasaur fragments, a possible *Trionyx*, and crocodile remains. The only other record of a specimen possibly assignable to this genus from New Jersey is a *Podocnemis* sp. recorded by Miller (1955, p. 907). Upon examination the material (ANSP 9370) is seen to consist of fragments which can be determined as being pelomedusid, but a generic identification is not possible.

The shell has not been subjected to distortion or compression. However, some sutures have been obscured by a limonitic cement. The plastron is nearly complete and well preserved. The left ilium and part of the right are preserved as well as a small portion of the pubis.

The ventral plates of the bridge peripherals (Fig. 6) in the Gulf shells are nearly as long as or slightly less than the dorsal plates. In the Merchantville turtle the ventral plates are about half as long as the dorsals. The hinder peripherals and pygal agree in outline with the southern forms, but a thick, ventral ridge, parallel to

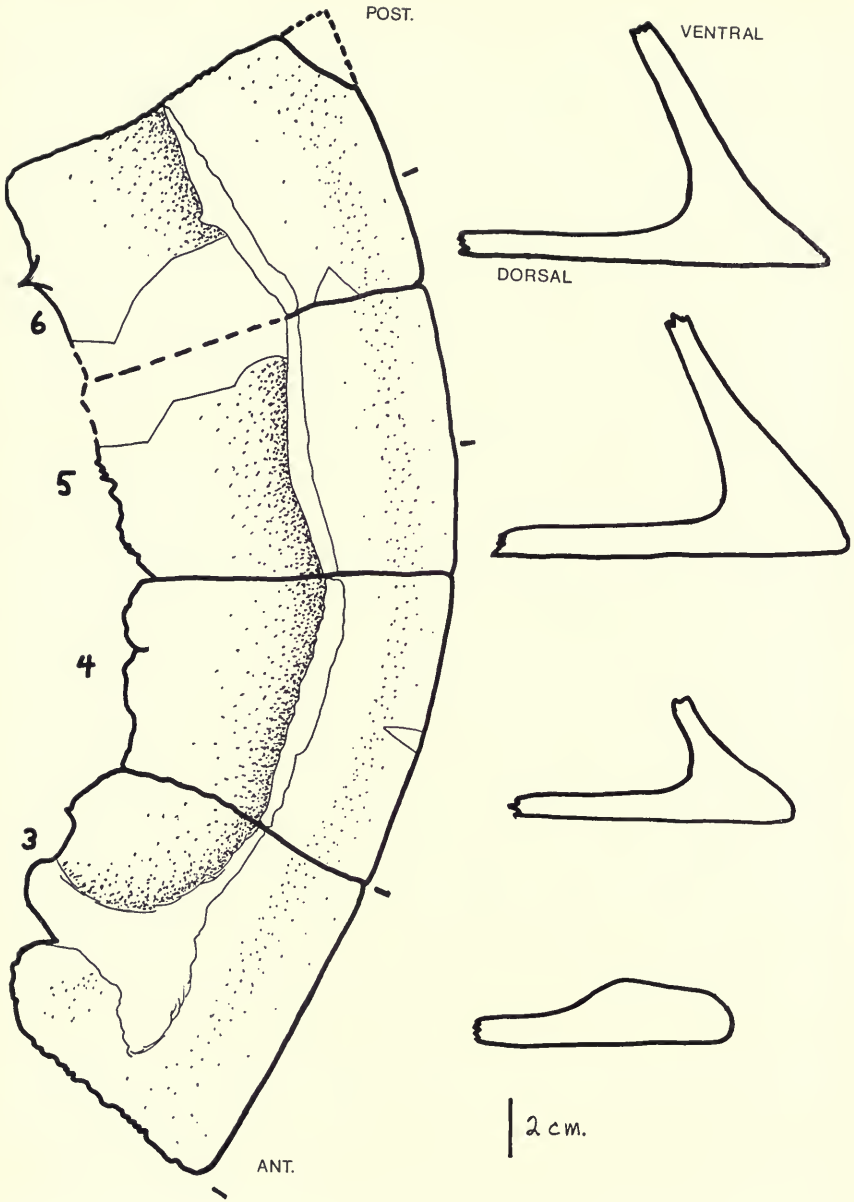


FIG. 6. *Bothremys barberi*, spp. A (ANSP 15902), Merchantville Formation, New Jersey, ventral view of right peripherals 3–6, sections made at points indicated by dashes.

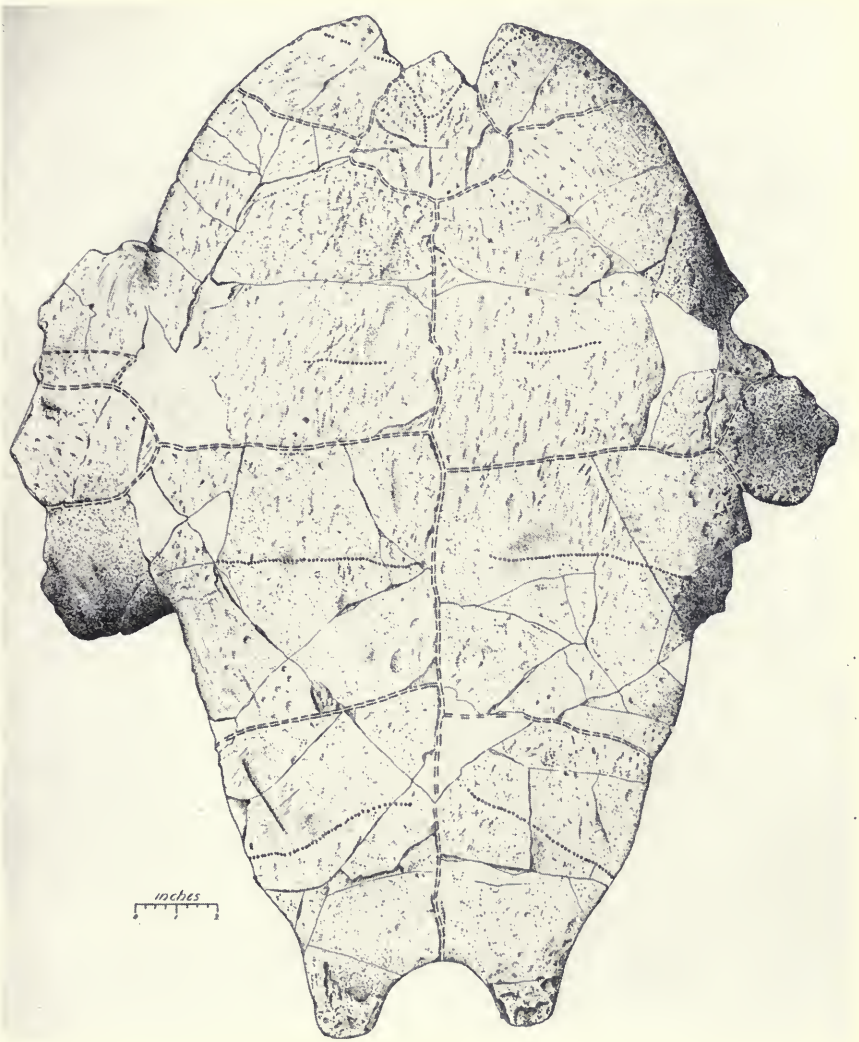


FIG. 7. *Bothremys barberi*, spp. A (ANSP 15902), Merchantville Formation, New Jersey, ventral view of plastron.

the edge of the carapace is developed on peripherals ten, eleven, and the pygal. This ridge is absent in the Gulf turtles. The sulci are determinable only in a few places and agree with previously described specimens of *B. barberi* (*Podocnemis alabamae* and *P. barberi*.) A small anomalous bone is present on the right bridge between mesoplastron and hyoplastron. The diagnostic features indicating the

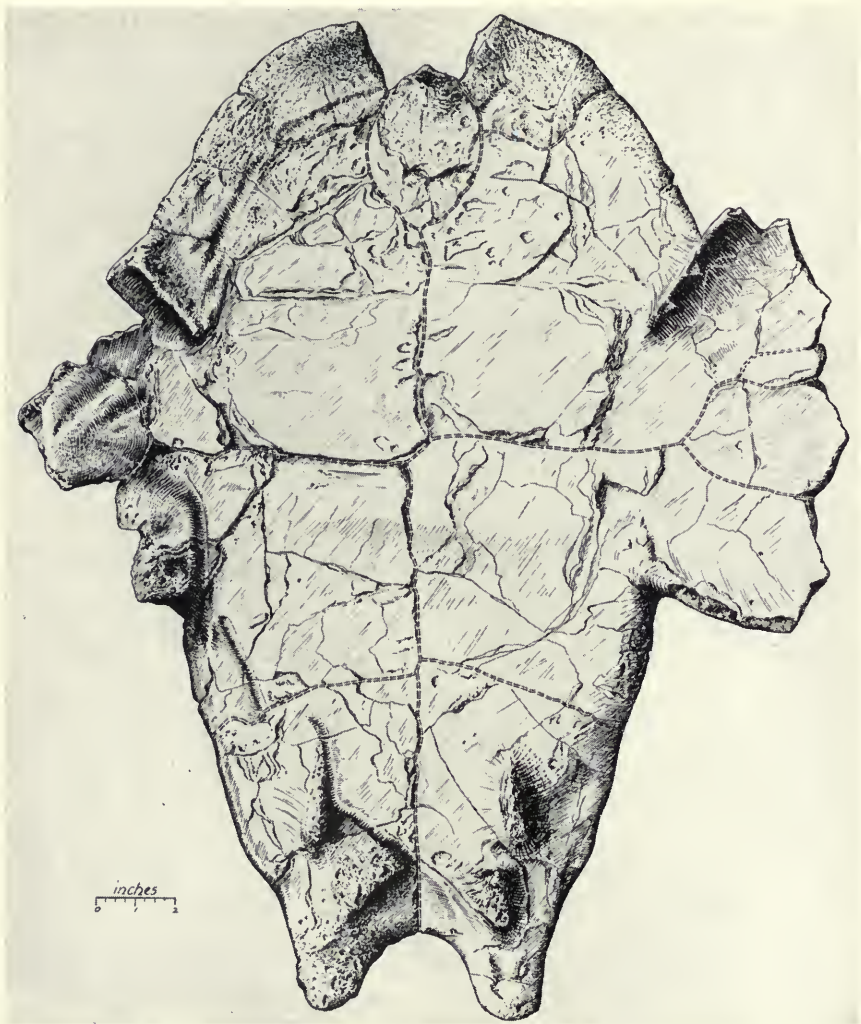


FIG. 8. *Bothremys barberi*, spp. A (ANSP 15902), Merchantville Formation, New Jersey, dorsal view of plastron.

generic identity of the Merchantville specimen with *Bothremys* may be summarized as:

1) costals 2-4 tend to be much shorter in relation to their width than in related genera;
2) anterior lobe of plastron short, broad and rounded;
3) posterior lobe long, tapering posteriorly;

FIG. 9. *Bothremys barberi*, spp. C (Peabody Museum 3608), Niobrara Formation, Kansas, dorsal view of carapace.

4) xiphiplastral notch broad and U-shaped, xiphiplastra end in rounded projections;
5) large, quadrilateral entoplastron;
6) pubic scar short and wide, ischiac scar triangular and separated from xiphiplastral edge.

SUBSPECIES B: THE GULF COASTAL PROVINCE

The forms described by Schmidt (1940) and Zangerl (1948) as *"Podocnemis barberi"* and *"P. alabamae"* make up this subspecies.

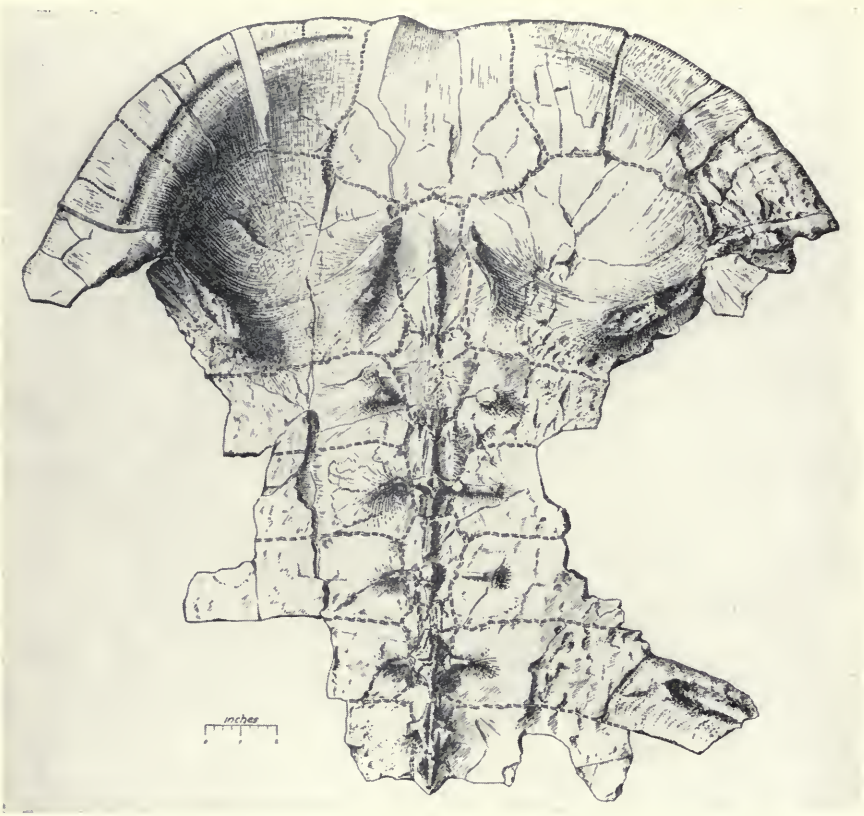


FIG. 10. *Bothremys barberi*, spp. C (Peabody Museum 3608), Niobrara Formation, Kansas, ventral view of carapace.

The new shell FMNH PR 247 (Figs. 2, 3) agrees with the previously described material from the Selma Formation.

SUBSPECIES C: THE EPICONTINENTAL PROVINCE

A shell in the Peabody Museum belongs to *Bothremys barberi* (Figs. 9–12). The specimen (Peabody Museum 3608) was collected in the Niobrara Formation of Wallace Co., Kansas, on June 14, 1876, by B. F. Mudge and party. It consists of a nearly complete plastron, lacking portions of the right bridge and portions of both xiphiplastra, as well as about 60 per cent of the carapace. The anterior end of the carapace is complete and includes the first two peripherals. Six neurals and the proximal portions of the first six costals are also preserved. The shell is crushed, causing the ridge area to lie flat in the plane of the plastron. The dorsal surface of the carapace is ex-

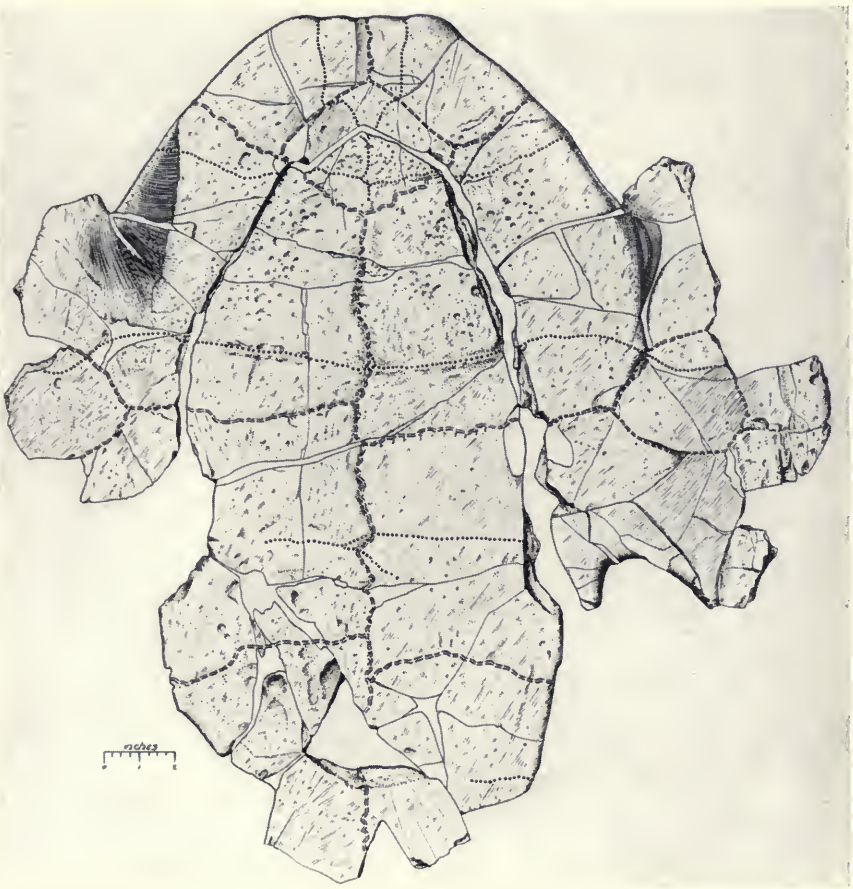


FIG. 11. *Bothremys barberi*, spp. C (Peabody Museum 3608), Niobrara Formation, Kansas, ventral view of plastron.

tensively damaged by deep pits, apparently of parasitic origin. Other evidences of parasitism are linear indentations on both plastron and carapace.

There are three main morphologic distinctions separating this specimen from the New Jersey and Gulf forms:

1) the nuchal is longer and narrower (in restoration the nuchal has been widened somewhat, so this is not as apparent in the figure as it should be);
2) the mesoplastra are equidimensional while in the other forms, width exceeds the length;
3) the epiplastral symphysis is relatively longer.

FIG. 12. *Bothremys barberi*, spp. C (Peabody Museum 3608), Niobrara Formation, Kansas, dorsal view of plastron.

The scale pattern agrees with the other specimens except for the anterior marginals which are nearly equidimensional, not wider than long as in the Gulf shells. An anomalous scale is present between the first vertebral and the first marginals. (Fig. 9).

A Miocene occurrence of Bothremys

A pelomedusid described by Collins and Lynn (1936, p. 155, plate I) as *Taphrosphys miocenica* seems to belong to the genus *Bothremys* instead. The type and only known specimen is the anterior portion of a plastron (USNM 13784) collected in 1934 from zone 10 of the

Calvert Formation, about one-fourth mile south of Camp Roosevelt, Maryland. Although the type cannot be found at present (Dr. Nicholas Hotton III, personal communication), the published figures and description are adequate to show that the specimen belongs to *Bothremys*. In *Taphrosphys* the large intergular separates the gulars, humerals, and part of the pectorals. It is not possible to determine the species since the type consists of such a small amount of material.

It should be emphasized that this specimen is the only North American pleurodire definitely known from Tertiary rocks. The genus *Taphrosphys* has been reported from the Lower Tertiary of New Jersey (Zangerl, 1948; Romer, 1956), but the stratigraphic data are questionable and specimens with good locality data are Cretaceous.

THE SKULL OF BOTHREMYS

INTRODUCTION

There are no pleurodires known from pre-Cretaceous sediments. Besides *Bothremys* the only Cretaceous pelurodiran skull materials known to the authors are fragments of *Taphrosphys* (being described by Gaffney) and undescribed Brazilian specimens being worked on by Price. The authors feel that since *Bothremys* has a well-preserved skull and since it is one of the oldest pleurodires, a rigorous description is necessary to provide a basis for comparison.

This description follows the anatomical nomenclature for turtle skulls standardized by Parsons and Williams (1961).

The material described here consists of a nearly complete skull with mandible (the type of *B. cooki*) and a partial skull with complete mandible (*B. barberi* FMNH PR 247). Where elements present in both skulls are described, *B. cooki* will be described first. The following recent material, belonging to the Department of Living Reptiles and Amphibians, American Museum of Natural History, served as comparative material in this study. The authors would like to thank Drs. Bogert and Zweifel for supplying these specimens.

F. Pelomedusidae:

Pelomedusa subrufa, AMNH 63581; *Pelusios gabonensis*, AMNH 10056; *Pelusios subniger*, AMNH 71188 and 10062; *Podocnemis expansa*, AMNH 58098 and 58194; *Podocnemis madagascariensis*, AMNH 63579; *Podocnemis unifilis*, AMNH 58195 and 58200.

F. Chelyidae:

Chelodina longicollis, AMNH 76569; *Chelus fimbriata,* AMNH 1117 (Vertebrate Paleontology Comparative Anatomy Collection); *Platemys platycephala,* AMNH 75101; *Emydura* sp., AMNH 72418; *Phrynops nasuta,* AMNH 58123 and 58110.

GROSS ASPECT

B. cooki

The type skull of *Bothremys cooki* (Figs. 13-16) lacks the posterolateral portions including occiput and quadrate, but the remainder is well preserved and undistorted.

In contrast to living pelomedusids, the skull of *Bothremys* is very wide, being about as wide as it is long (excluding crista supraoccipitalis). This width is due principally to the presence of large paired pits in the triturating surfaces. The short face is comparable to living pelomedusids, but the orbits are farther apart and face more dorsad in *Bothremys.*

The bones roofing the *fossa temporalis* are missing. There is no indication of emargination, the posterior limits of the skull roof being represented by broken edges. The orbits are nearly circular and face antero-dorsolaterad.

The dorsal surface of the skull is horizontal posteriorly, sloping somewhat anteriorly. There is a slope of about 25 degrees from between the orbits to the *apertura narium externa.* The *apertura* is preserved best on the right side but still lacks the medial-most parts. The opening has the shape of a figure eight lying on its side, similar to *Podocnemis expansa* but lower and wider. There is no conclusive evidence against the possibility that a thin septum was present medially. The anterolateral surface of the skull is broad and convex outward.

The triturating surfaces of the palate are narrow anteriorly and expand posteriorly and laterally to accommodate the huge pits present between the lingual and tomial margins. The area between the lingual ridges consists of a shallow median trough containing the paired *aperturae narium internae* and the *foramina praepalatina.*

Processus pterygoidei externi are present on the pterygoids, but since they are broken laterally their complete extent is not known. The margins of the *fenestra subtemporalis* as preserved are roughly comparable to those of *Podocnemis expansa.* The *processus articularis* of the quadrate and *condylus occipitalis* are not preserved.

B. barberi

The *processus articularis* is placed farther posteriorly than in the living pleurodires. The *cavum tympani* has a closed posterior margin and is well developed. The *incisura columellae auris* is a highly ossified canal. The *fenestra postotica* cannot be determined.

No indication of sulci can be seen on the surface of either skull. The dorsal surface of the parietals in *B. cooki* has a series of fine branching grooves, many ending in small foramina (Fig. 14B). This sort of surface may also be seen in *Podocnemis*.

PARIETAL

B. cooki

The paired parietals (Figs. 13, 14, 18) cover the median part of the posterior skull roof. They meet the frontals anteriorly in a transverse suture and the postorbitals more laterally as in the living pelomedusids. The lateral and posterior portions are represented by broken edges; no indications of emargination are preserved.

The vertical component of the parietal (Figs. 13, 14, 16, 17) consists of two pairs of plates, one pair on each side, which join dorsally to form one pair meeting the horizontal component of the parietal. Anteriorly the medial plate (*processus inferior parietalis*) is sutured to the palatine near the posterior edge of that bone and borders the relatively reduced orbito-cranial passage (no term available in Parsons and Williams, 1961). Farther posteriorly the parietal meets the *crista pterygoidea* in a long, horizontal suture that ends posteriorly at the *foramen nervi trigemini*. This foramen is bordered dorsally by the parietal, but this bone contributes to less than one-fourth of the circumference of the foramen. The most posterior suture is with the supraoccipital.

The more lateral process of the parietal (Figs. 16, 17) diverges from the *processus inferior parietalis* antero-ventrally and meets a flange from the postorbital antero-laterally. It probably had a contact with the pterygoid, but this area is now missing.

The ventral region of the parietal in living pelomedusids consists principally of only one pair of vertical plates. The lateral plate, which in *Bothremys* is formed by the parietal, consists of the postorbital, palatine, pterygoid, and sometimes parietal in the living genera.

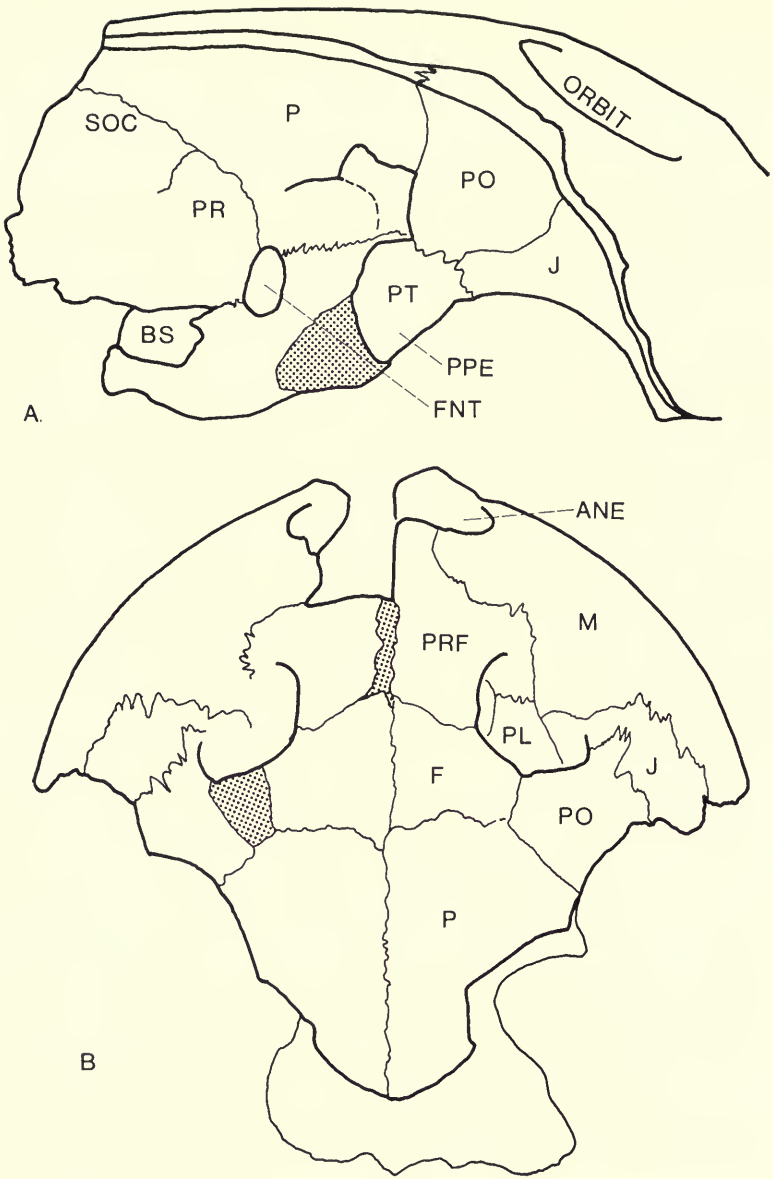


FIG. 13. *Bothremys cooki* (type skull), ?Hornerstown Formation, New Jersey. A, postero-lateral view (see Fig. 14A). B, dorsal view (see Fig. 14B). ANE - *apertura narium externa*, BS - basisphenoid, F - frontal, FNT - *foramen nervi trigemini*, J - jugal, M - maxilla, P - parietal, PL - palatine, PO - postorbital, PPE -- *processus pterygoideus externus*, PR - prootic, PRF - prefrontal, PT - pterygoid, SOC - supraoccipital.

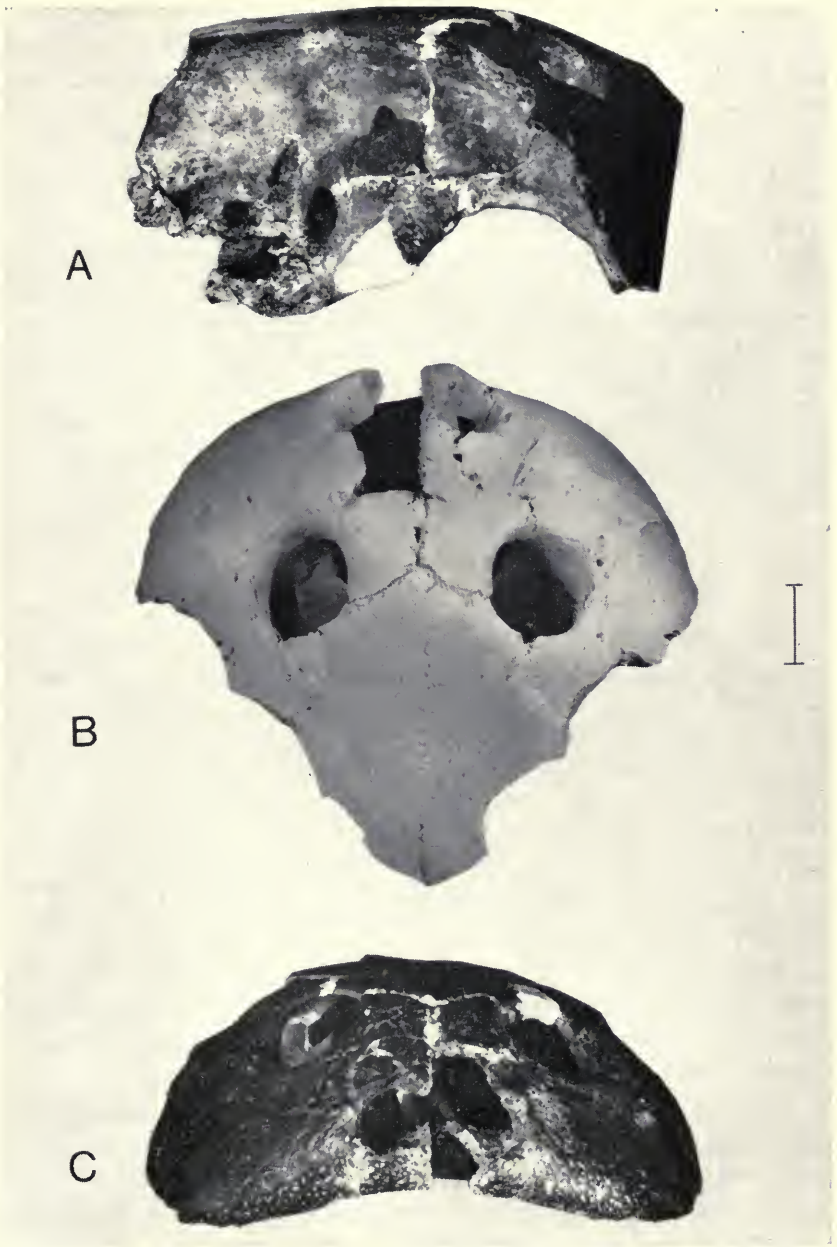


FIG. 14. *Bothremys cooki* (type skull), ?Hornerstown Formation, New Jersey. A, postero-lateral view. B, dorsal view. C, anterior view. Scale - 1 cm.

The medial portions of the parietals are preserved in *B. barberi* and agree with *B. cooki* except for being relatively thicker and more massive.

FRONTAL

B. cooki and *B. barberi*

The frontal (Figs. 13, 14) is a quadrilateral element meeting, from front to back, the prefrontal, orbits, postorbital, and parietal. On the ventral surface a triangular ridge defines the *sulcus olfactorius* (Fig. 17). The frontal has about half the length of the prefrontal or parietal, being relatively smaller, but otherwise quite similar, to the living pelomedusid genera. There is no longitudinal groove on the dorsal surface as in South American *Podocnemis*, with the exception of *P. dumeriliana*.

PREFRONTAL

B. cooki

The prefrontal (Figs. 13, 14) is a long, somewhat irregular element, sutured posteriorly to the frontal. It forms the antero-medial margin of the orbit and contributes to about one-third of its circumference. Only the right prefrontal is preserved anteriorly, and the limits of the bone in this area are somewhat ambiguous. As we interpret it, the prefrontal meets the maxilla in an irregular suture beginning at the dorsal part of the *apertura narium externa* and running postero-laterally to the ventral edge of the orbit.

On the ventral surface the *sulcus olfactorius* continues for a short distance on the prefrontal.

Bothremys has a short process descending ventrally along the inner margin of the anterior orbital rim which meets the palatine ventrally. In living pelomedusids this process no longer reaches the palatine.

The orbito-cranial passage is very large in living pelomedusids but is restricted in *Bothremys* because the skull roof, and consequently the *sulcus olfactorius* and *processus inferior pterygoideus*, are very low. Also, the vomer rises above the level of the palate, further restricting the *fissura ethmoidalis*.

The *foramen orbito-nasale* is not distinct from the *fossa nasalis*, that is, the prefrontal does not descend to meet the vomer in the midline. This condition is characteristic of all pleurodires.

POSTORBITAL

B. cooki

The postorbital (Figs. 13, 14) consists of two plates at right angles to each other. The dorsal plate meets the jugal antero-laterally, the orbit antero-medially, the frontal medially, the parietal postero-medially, and has a broken edge postero-laterally. The original posterior extent of the postorbital is not known. Ventrally the postorbital consists of a vertical plate, diverging anteriorly about 45 degrees from the skull midline. This plate has a long union with the jugal antero-laterally, reaches the pterygoid postero-ventrally and meets the lateral vertical process of the parietal posteriorly. The parietal union is not preserved for half its ventral length.

The postorbital of living pelomedusids differs from *Bothremys* principally in being less developed ventrally and contributing less to the anterior wall of the temporal fossa.

JUGAL

B. cooki

The jugal has a fairly limited exposure dorsally, but its ventral surface forms the pit so characteristic of this animal (Figs. 15, 16, 20). If removed from the surrounding bones, the jugal is somewhat cone-shaped. Anteriorly the jugal meets the maxilla in an extensive and complex pattern.

A well developed buttress extends antero-laterally from the cone-shaped area of the jugal to the medial surface of the maxilla. The posterior corner of this process abuts against the *processus pterygoideus externus* of the pterygoid. Ventrally a thin sheet of palatine covered the jugal-pterygoid suture, but is now broken off. Above this suture the entire posterior edge of the jugal lies against the postorbital. Medial to the pterygoid contact there is a short suture with the palatine. In front of this the maxillary suture begins.

The dorsal plate of the jugal lies between the maxilla and postorbital, and borders the orbit. The posterior-most edge is broken.

In living pelomedusids, the area homologous to the pits in *Bothremys* faces posteriorly into the subtemporal cavity and does not enter onto the triturating surface. This condition also prevails in amphichelydians, and, in fact, in most reptiles. A complex (but unknown) series of evolutionary events must have taken place to make this area available as a triturating surface.

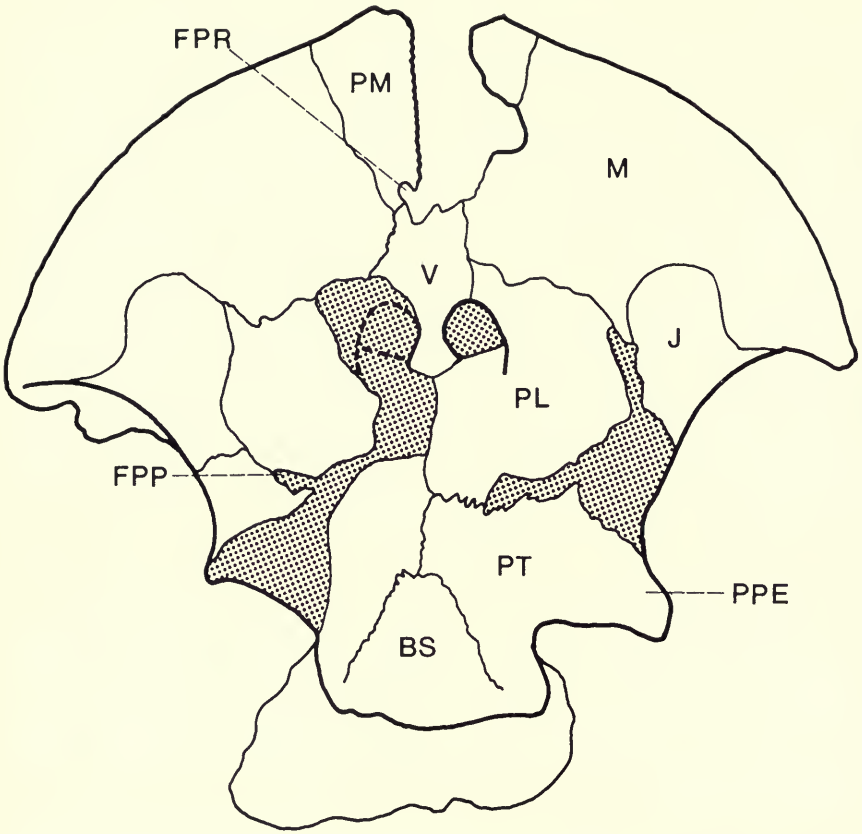


FIG. 15. *Bothremys cooki* (type skull), ?Hornerstown Formation, New Jersey, ventral view of skull. Abbreviations also for Figures 16 and 17. BS - basisphenoid, CL - *cavum labyrinthicum*, FNT - *foramen nervi trigemini*, FPP - *foramen palatinum posterius*, FPR - *foramen praepalatinum*, ICA - *incisura columellae auris*, J - jugal, LP - lateral process of parietal (see text under Parietal), M - maxilla, PIP - *processus inferior parietalis*, PL - palatine, PM - premaxilla, PPE - *processus pterygoideus externus*, PT - pterygoid, SF - *sulcus olfactorius*, SO - supraoccipital, V - vomer. Dotted areas are restored.

PREMAXILLA

B. cooki

Most of the right premaxilla is lost and the antero-medial part of the left premaxilla is broken. The premaxilla (Fig. 15) is roughly triangular in shape, being widest anteriorly, and forms the floor of the *apertura narium externa*. Laterally it is sutured to the maxilla for most of its length, but there is a short meeting with the vomer

at the posterior end of the premaxilla. Just slightly anterior to the vomerine suture and close to the midline lies the *foramen praepalatinum*. The postero-medial edge of the foramen is missing, and it is not known whether it was completed by the premaxilla, maxilla or vomer.

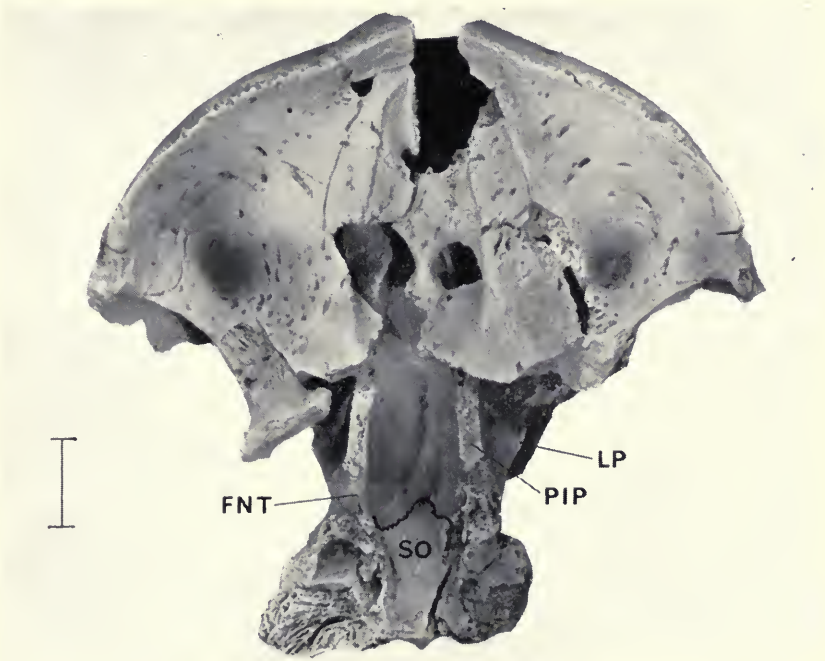


FIG. 16. *Bothremys cooki* (type skull), ?Hornerstown Formation, New Jersey, ventral view of skull with basisphenoid and most of pterygoids removed. Scale - 1 cm. See Figure 15 for abbreviations.

On the dorsal surface a raised area begins medially and anteriorly but is missing farther in that direction, and it cannot be determined if this separated the external nares.

A very thick tomial ridge is present on the ventral surface, and a groove divided it from the shallower lingual ridge. Laterally, the lingual ridge turns sharply backward. Many foramina penetrate the triturating surface. In the midline a U-shaped groove, formed between the lingual ridges, widens posteriorly.

The premaxilla protrudes anteriorly from the face in a manner similar to the same bones in *Podocnemis expansa*.

MAXILLA

B. cooki

Earlier authors (Leidy, 1865; Hay, 1908) described the maxilla as including the palatal pits. This study has revealed the fact that the pits are formed by the jugals.

The maxilla (Figs. 13-16) may be divided into two main areas: a curved anterior portion, somewhat vertical and exposed externally on the cheek and a more horizontal portion sutured to the bones of the palate and lying internal to the face. The external part meets the premaxilla anteromedially and forms the lateral border of the *apertura narium externa*. From the *apertura* to the orbit, there is an irregular suture with the prefrontal. The maxilla forms a small part of the orbital margin ventrally, meets the jugal dorso-laterally, and ends in a broken edge posteriorly.

Anteriorly, the vertical portion of the maxilla is sutured to the premaxilla and forms the floor of the *fossa nasalis* lateral to the premaxilla and vomer. Posterior to the premaxilla the maxilla has a short antero-posterior union with the vomer. At the junction with the vomer, the palatino-maxillary suture turns laterad in the direction of the jugal pit. The maxilla meets the jugal just medial to the pit and has a semi-circular course anteriorly around the pit.

The maxilla bears only a small portion of the labial ridge. The ventral surface lateral to the labial ridge and the anterior edge of the tomial ridge bear many nutritive foramina. The surface between the labial and tomial ridges curves sharply into the deep jugal pit.

Opening onto the internal surface of the maxilla at the lateral edge of the *fossa nasalis* lies the *foramen alveolare superius*.

PALATINE

B. cooki

Neither palatine is complete, but from surrounding bones the limits may be determined. The palatine (Figs. 15, 16) has two vertical surfaces which join laterally to form one sheet. Between these surfaces medially lies the *apertura narium interna*. In front of the *apertura* there is a short suture with the vomer; behind the *apertura* the palatines meet each other for most of their length. The palatine meets the maxilla anteriorly, the jugal laterally, and pterygoid posteriorly. In tranverse section the medial portion is C-shaped around the *apertura*. The dorsal edge of the *apertura* is more posterior than the ventral edge.

The labial ridge runs diagonally, antero-medially to postero-laterally, across the palatine. The triturating surface has many foramina and slopes up into the jugal pit. The medial surface has no foramina and bends around onto the *apertura.*

On the dorsal surface a short posterior process rises to meet the anterior part of the *processus inferior parietalis.* Between this articulation and the dorsal edge of the *apertura* lies a small foramen which does not seem to penetrate the ventral surface.

The palatine forms most of the posterior part of the orbital floor.

The *foramen palatinum posterius* penetrates the suture between the palatine and the pterygoid about midway along the suture's width, as in the living pelomedusid genera.

The overall relations of the palatine in *Bothremys* are quite similar to the condition in recent pelomedusids except for the presence of a vomer in *Bothremys.* An internarial septum may be formed in the recent genera by an anterior extension of the palatines in the midline.

VOMER

B. cooki

The vomer (Figs. 15, 16), a thin, medial element, extends from the posterior junction of the premaxillae to the palatines and separates the *aperturae narium externae.* Its anterior end is broken so the exact relations with the premaxillae are unknown, and it is possible that the vomer formed part of the margin of the *foramen praepalatinum.* Laterally, anterior to the *aperturae* the maxillae meet the vomer in a fore-and-aft suture. The anterior half of the vomer widens posteriorly to the *aperturae* where it narrows between the two openings. The posterior end expands to meet the palatines, but does not become as wide as the anterior half.

The vomer is higher than wide in cross-section and has a shallow groove, the *sulcus vomeri,* running along its dorsal surface from front to back.

The posterior half of the vomer rises dorsally above the level of the median trough in the palate.

The vomer is absent in living pelomedusids except *Podocnemis vogli* (Williams, 1954b, pp. 289, 291), but it is present in most chelyids and amphichelydians. The vomer of *Bothremys* is more like that bone in amphichelydians (particularly *Chisternon hebraicum,* AMNH 5961, from figures by Hay, 1908) than in *Podocnemis vogli.* The importance of this distinction is debatable.

PTERYGOID

B. cooki

The pterygoids (Figs. 15, 19) are broken posteriorly and laterally; their limits are unknown in this region in *B. cooki*. These elements meet sagittally for about half their preserved length and have a transverse suture with the palatines anteriorly. The small *foramen palatinum posterius* penetrates the palate at the palatine-pterygoid suture as in modern pelomedusids.

The *processus pterygoideus externus* meets the jugal anteriorly beneath a thin covering of palatine now broken off and extends posteriorly and laterally to form a process which, although poorly preserved, is comparable to that seen in the living pelomedusid genera. The outer scroll-like portion is not preserved but the thicker, more medial part is preserved and is essentially like that in *Podocnemis*.

Ventrally, the triangular basisphenoid lies between the posterior halves of the pterygoid. A shallow groove parallels the basisphenoid-pterygoid suture lateral to that suture on the ventral surface of the pterygoid.

Dorsally, the pterygoids underlie the *rostrum basisphenoidale* anteriorly and extend posteriorly around the main body of the basisphenoid. The anterior limits are the same as on the ventral surface but the posterior suture cannot be determined. The *crista pterygoidea* is fairly low but rises posteriorly. The *foramen nervi trigemini* is much lower than in the living forms and cuts into the *crista pterygoidea* down to the level of the *sulcus cavernosus*. In *Podocnemis* the foramen is rather high, while in *Pelusios* and *Pelomedusa* it is lower but not at the level of the *sulcus cavernosus*. The sulcus itself is quite wide, comparable in size to that seen in *Podocnemis madagascariensis*. A posterior pair of foramina, in the position of the *foramen pro ramo nervi vidiani* is present in *B. cooki* but could not be probed, so the actual identification is dubious. Another foramen penetrates the medial edge of the right pterygoid anterior to the above foramina; its purpose is unknown.

The enlarged "carotid canal" (Siebenrock, 1897; Williams, 1954a) characteristic of the genus *Podocnemis* is absent in *Bothremys*.

B. barberi

The Selma specimen, although in much worse condition, does preserve the postero-medial limits of the pterygoids (Fig. 19). The area is crushed, weathered, and has poorly defined sutures.

The pterygoid of living pelomedusids extends posteriorly less than half the length of the basisphenoid. The pterygoid of the type specimen extends at least as far back as the end of the basisphenoid, and the Selma specimen shows the pterygoids reaching the preserved limits of the basioccipital (which includes most of the condyle).

The enlarged carotid canal of *Podocnemis* (Fig. 19) is absent, and there is an indication of a quadrate connection to the basisphenoid and possibly to the basioccipital.

The pterygoid of living pelomedusids does not floor any part of the *fenestra postotica*, but, due to the posterior extension of this bone in *Bothremys*, it may have underlain part of this cavity. However, the area is badly damaged or missing, and this cannot be verified.

The *foramen posterius canalis carotici interni* as well as the relationship of the pterygoid to the exoccipital and opisthotic are not determinable.

BASISPHENOID

B. cooki

The posterior and postero-lateral limits of the basisphenoid (Fig. 19) are unknown. It has a triangular shape ventrally with the apex cut by a short transverse suture. The preserved posterior edge may be the actual one, but being badly damaged this cannot be determined. Its anterior and lateral boundaries are sutured to the pterygoids.

Dorsally, the *rostrum basisphenoidale* extends anteriorly over the sagittal suture of the pterygoid to the posterior limits of the palatines. The *sella turcica* is very deep and somewhat overhung by the *dorsum sellae* much as in the three living genera (except *Podocnemis madagascariensis*). In the lateral wall of the *sella turcica* lies the large paired *foramen anterius canalis carotici interni*. The *processus clinoideus* is absent in *Bothremys* but present in the specimens of living pelomedusid genera examined by us (although it is reduced in *Pelusios gabonensis*). Posterior to the *dorsum sellae* the basisphenoid is a concave plate.

The area of the *cavum labyrinthicum* and *hiatus acusticus* is badly damaged and undeterminable. No other foramina are preserved.

B. barberi

Although most of the basisphenoid is preserved in this specimen, the preservation is so poor that little more can be added.

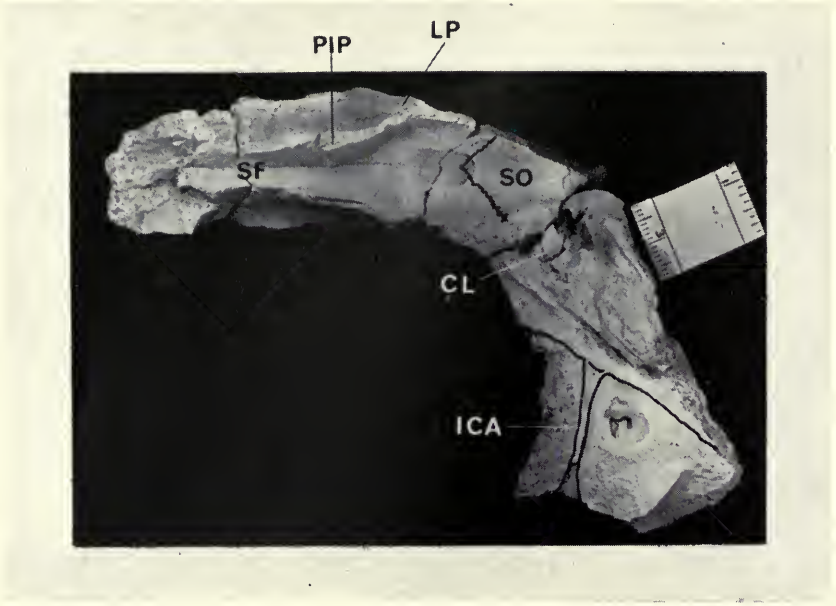


FIG. 17. *Bothremys barberi*, spp. B (FMNH PR 247), Selma Formation, Alabama, ventral view of interior of cranial cavity and right otic region. Left side of scale is in millimeters. See Figure 15 for abbreviations.

The acustic hiatus is at the posterior end of the basisphenoid on the basioccipital suture. The ventral suture with the basioccipital can also be seen. It curves anteriorly and is similar to that in *Podocnemis*. The postero-lateral limits cannot definitely be determined, but there seems to be contact with the quadrate.

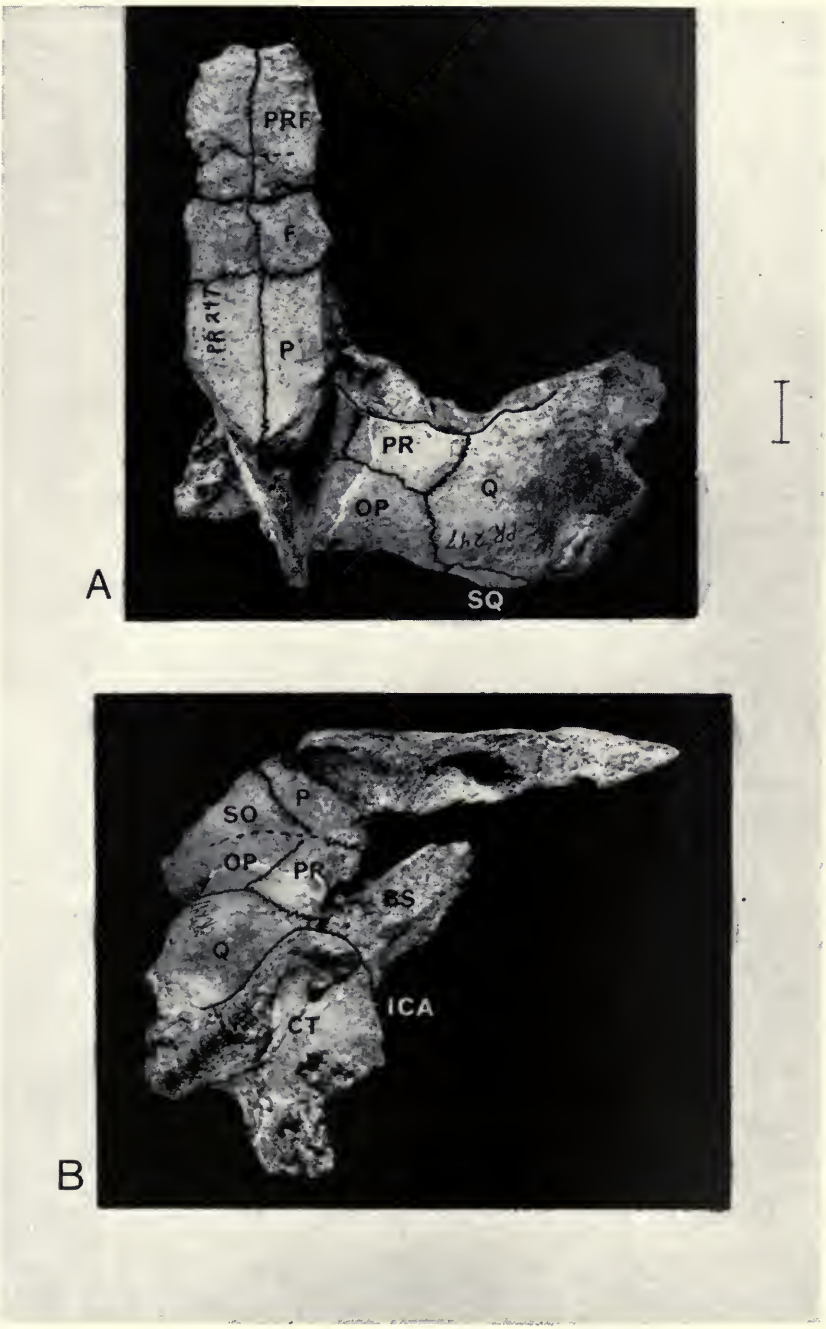
The rest of the specimen agrees with the type except for the shallower *sella turcica* which may be due to breakage.

BASIOCCIPITAL

B. barberi

Dorsally the basioccipital is a small triangular element with the apex pointing posteriorly. It has a transverse suture anteriorly

FIG. 18. *Bothremys barberi*, spp. B (FMNH PR 247), Selma Formation, Alabama, skull table fragment and right otic process. A, dorsal view. B, lateral view. BS - basisphenoid, CT - *cavum tympani*, F - frontal, ICA - *incisura columellae auris*, OP - opisthotic, P - parietal, PR - prootic, PRF - prefrontal, Q - quadrate, SO - supraoccipital, SQ - squamosal. Basisphenoid has been crushed upward. Scale - 1 cm.


PRF
F
P
PR
Q
OP
SQ
A
SO
P
OP
PR
BS
Q
ICA
CT
B

with the basisphenoid and postero-lateral sutures with the two exoccipitals. It is excluded from the foramen magnum by the exoccipitals.

Ventrally there is an anterior suture with the basisphenoid which curves anteriorly as in the living forms. The precondylar fossa is delimited by this suture and is wider than long. The posterior surface and condylar area are badly eroded and sutures cannot be determined. *Pelusios* and *Pelomedusa* lack this fossa which is best developed in *Podocnemis*, particularly *P. expansa*. This area in *Bothremys* is similar to *P. expansa* and differs principally in being shorter. The quadrate may possibly articulate with the lateral extension of the basioccipital, but the sutures are badly obscured, and this seems unlikely.

The *tubercula basioccipitalia* are large and prominent in *Podocnemis* but absent in *Pelusios* and *Pelomedusa*. This area in *Bothremys* is difficult to interpret, but the *tubercula* seem to be lacking entirely.

SUPRAOCCIPITAL

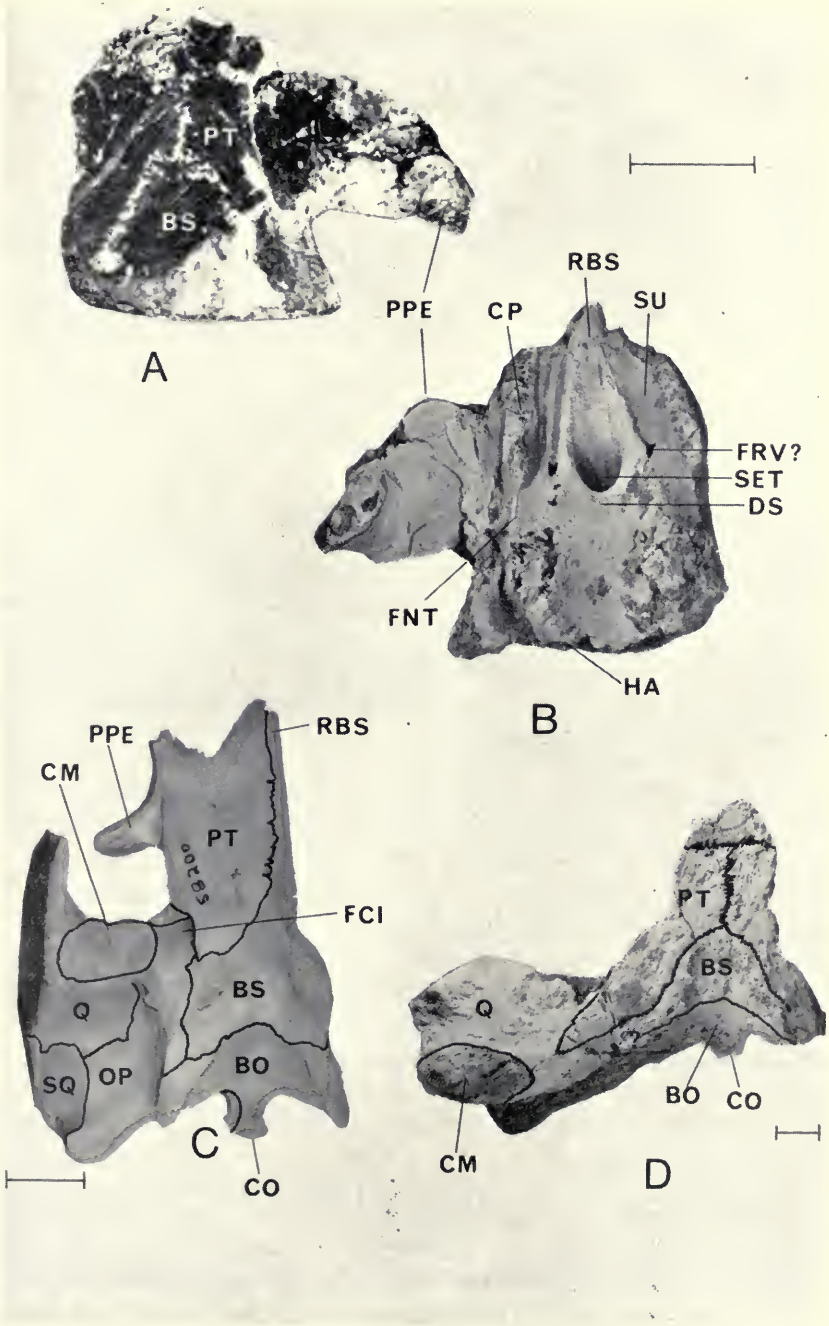
B. cooki

The supraoccipital (Figs. 13, 14, 16) lacks most of its posterior portion (including the *crista supraoccipitalis*), and its anterior relations are obscured by damage from pyrite decomposition.

On the ventral surface the supraoccipital has a diagonal suture with the parietal trending posteriorly from the midline. This suture turns anteriorly on the medial edge of the *foramen nervi trigemini*. The actual edge of the foramen, however, is bordered by the parietal dorsally, the prootic posteriorly, and the pterygoid ventrally. The relations of the prootic to the supraoccipital in this area are not clear. The supraoccipital has long interdigitations along its anterior edge with the parietal and prootic, which makes suture determination difficult in eroded areas.

The *recessus labyrinthicus supraoccipitalis* is preserved on the left side. The *crus commune* is contained here as well as the dorsal portions of the *canalis semicircularis anterior* and the *canalis semicircularis posterior*. The upper edge of the *hiatus acusticus* is badly broken.

FIG. 19. A, B, *Bothremys cooki* (type skull), basisphenoid and pterygoids. A, ventral. B, dorsal. C, *Podocnemis unifilis* (AMNH 58200), recent, South America, ventral view of right posterior portion of skull. D, *Bothremys barberi* (FMNH PR 247), same region as C. Scale - 1 cm. Abbreviations on page 236.


PT
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D

Externally only the most anterior part of the supraoccipital is preserved. It articulates with the parietal dorso-anteriorly. Its other sutures cannot be determined adequately.

B. barberi

The supraoccipital (Figs. 17, 18), agrees with *B. cooki*. The dorsal sutures, however, are slightly better preserved. The parietal-supraoccipital suture is directed more ventrally than in *B. cooki*. The ventral margin has a crushed contact with the opisthotic and may have met the posterior edge of the prootic.

OPISTHOTIC

B. barberi

The opisthotic meets the prootic anteriorly in a long suture, the quadrate dorso-laterally, the squamosal postero-laterally, and the supraoccipital medially. The area of this last suture is badly broken and pushed up onto the supraoccipital. Relations with the exoccipital are unknown.

Ventrally (internally), the opisthotic (Fig. 17) forms the posterior wall of the labyrinth. A broken *processus interfenestralis* may be seen, but further details cannot.

PROOTIC

B. barberi

The right prootic (Fig. 18) is crushed and poorly preserved; the left one is absent. Dorsally, the prootic has a short suture with the parietal antero-medially, the quadrate laterally, the opisthotic posteriorly, and (?) the supraoccipital postero-medially. Ventrally (Fig. 17) the semi-circular canals are preserved. The prootic forms the anterior wall of the labyrinth, but details such as the *fossa acustico-facialis* cannot be seen. No additional information can be obtained from *B. cooki*.

QUADRATE

B. barberi

Only the right quadrate (Figs. 17, 18, 19) is preserved. It has been crushed and probably distorted, but the more important relationships are determinable. The anterior, posterior, and lateral

edges are eroded, and the bone is split through the middle revealing some of the internal structure.

The quadrate is relatively more extensive laterally than in living pelomedusids. The anterior edge has been eroded back to the *foramen stapedio-temporale*. The medial border is sutured to the prootic anteriorly and the opisthotic posteriorly. The posterior margin is badly broken, but there seems to be a small portion of the squamosal preserved just lateral to the posterior termination of the opisthotic-squamosal suture. The whole lateral edge is represented by an eroded surface.

Much of the ventro-medial structure is obscured by crushing in which the basicranium has been pushed dorsally and laterally into the otic extension. The existence of a *processus trochlearis* is not known. The form of the *cavum acustico-jugulare* is not determinable.

At the postero-ventral extension of the quadrate lies the *processus articularis* (Fig. 19). It has a greater ventral extent than in living pelomedusids. Furthermore, one of the chief differences between *Bothremys* and the living genera is the posterior position of the *processus articularis* in the extinct genus. Modern pelomedusids have the articulation quite forward of the occipital condyle, in fact, well anterior to the basioccipital. In *Bothremys*, however, the *processus articularis* is in the same vertical plane with the occipital condyle, a condition similar to amphichelydians, and, therefore, probably primitive. Much of the actual articulating surface, the *condylus mandibularis*, is eroded, but its shape can be determined. It had the form of an elongate oval and did not seem to be sharply concave as in the recent forms, but slightly concave or flat.

Just medial to the *processus articularis* is the postero-lateral extension of the pterygoid which forms a process buttressing the quadrate.

The edges of the *cavum tympani* (Fig. 18) are eroded and broken so its complete extent is not known. As preserved, it is an oval depression with a foramen near its anterior border. Internally, it can be seen that this foramen is the *incisura columellae auris*, in this case, actually a *canalis* because of the posterior closure of the quadrate. It is far removed from the posterior edge of the *cavum* and is more ossified than in any other pleurodire. Slightly posterior to the stapedial opening is a small indentation, possibly a post-otic antrum, but the area is poorly preserved. The *cavum tympani* also contains a large trough that extends postero-ventrally from the *in-*

cisura and medially behind the quadrate to the vicinity of the *fenestra postotica*.

A fracture through the middle of the otic region has exposed some internal details (Fig. 17). The *incisura columellae auris* extends from the lateral surface of the quadrate medially to a canal,

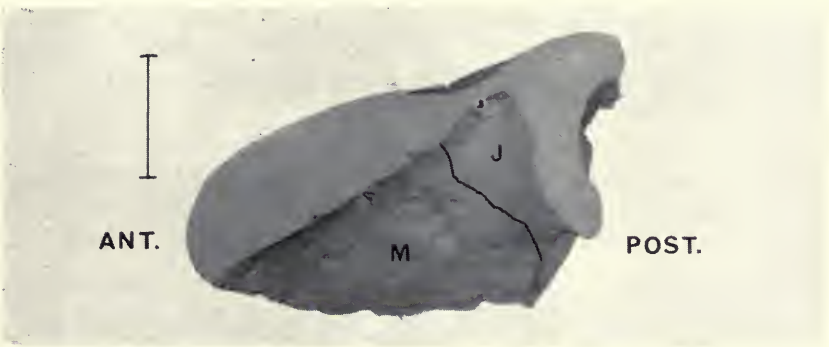


FIG. 20. *Bothremys cooki* (type skull), ?Hornerstown Formation, New Jersey, cross-section through a cast of the right palatal pit. J - jugal, M - maxilla.

which probably represents the *cavum acustico-jugulare*. The region is not sufficiently well preserved to compare with other forms.

ENDOCRANIAL CAST

Endocranial casts (Fig. 21) of latex were made from both specimens. Although it is generally true that reptilian endocasts do not reflect much detail of the brain itself, they are informative to some extent.

The endocranium of *B. cooki* is best preserved and its cast may be compared with a similar cast of *Podocnemis madagascariensis*. As Edinger (1929) has shown, the first principal flexure generally delimits the cerebral area from the olfactory region. The *sulcus olfactorius* which extends anteriorly from this flexure is wide in *Bothremys* and narrow in *P. madagascariensis*. The sides of this trough are also more extensive in the extinct genus. The cerebral expansions are similar in both but wider in *Bothremys*. The unossified anterior portion of the supraoccipital has left a "rider" on top of the cerebral area (see Zangerl, 1960, p. 290). Just behind the hemisphere region and below the "rider" is a low dorso-ventral groove leading to the *foramen nervi trigemini*.

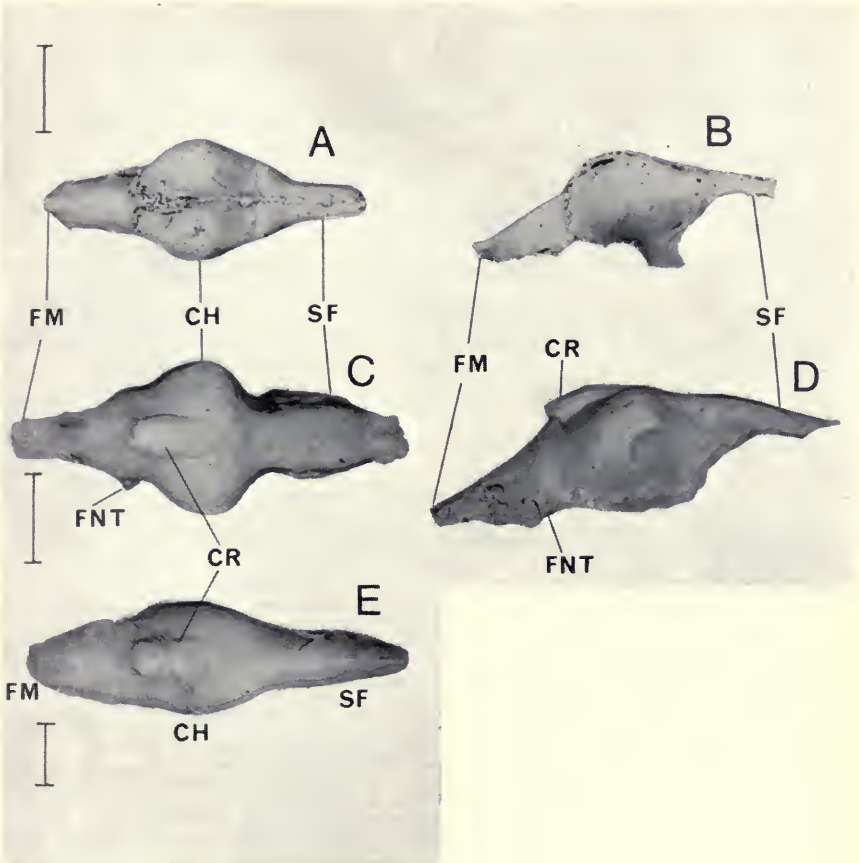


FIG. 21. Endocranial casts, A, C, E, dorsal view; B, D, lateral views. A, B, *Podocnemis madagascariensis* (AMNH Living Reptiles 63579). C, D, *Bothremys cooki* (type skull). E, *Bothremys barberi* (FMNH PR 247). CH - region of cerebral hemispheres, CR - cartilaginous "rider" fill (see text), FM - position of *foramen magnum*, FNT - *foramen nervi trigemini*, SF - *sulcus olfactorius*. Scale - 1 cm.

The endocranium of *Bothremys barberi* has less preserved along the sides, but comparisons can be made. It differs from *B. cooki* in having much less pronounced cerebral expansions and a relatively smaller *sulcus olfactorius*. The differences are greater between *B. cooki* and *B. barberi* than between *B. cooki* and *P. madagascariensis*. This apparent anomaly may be explained by the absolute size difference in the extinct skulls. Reptilian brains tend to be relatively smaller in larger animals. *B. barberi* is twice the size of *B. cooki*, but the brains were probably only slightly different in size (if recent

reptiles are a correct analogy). Therefore, although the brains were probably very similar, the cavities housing them are not.

MANDIBLE

B. cooki

The posterior parts of the jaw (Fig. 22), including articular surfaces, have been broken off. The specimen has suffered from pyrite decomposition and none of the sutures are distinguishable.

The most obvious features are the large pits that occupy most of the jaw. These excavations open anteriorly and extend posteriorly as conical cavities well beneath the coronoid processes. The whole anterior half of the jaw is concerned with forming these pits.

There is no distinct ridge anteriorly; the surface is essentially horizontal. Posteriorly the labial margin curves upward and forms the lateral side of the trumpet-shaped pit. The tomial ridge begins near the symphysis and extends posteriorly and dorsally, forming the medial edge of the pit.

The symphysis is tightly fused. It is much thicker posteriorly than anteriorly, forming a triangular cross-section.

The coronoid process is quite high and well developed. It is rounded dorsally and somewhat longer than wide.

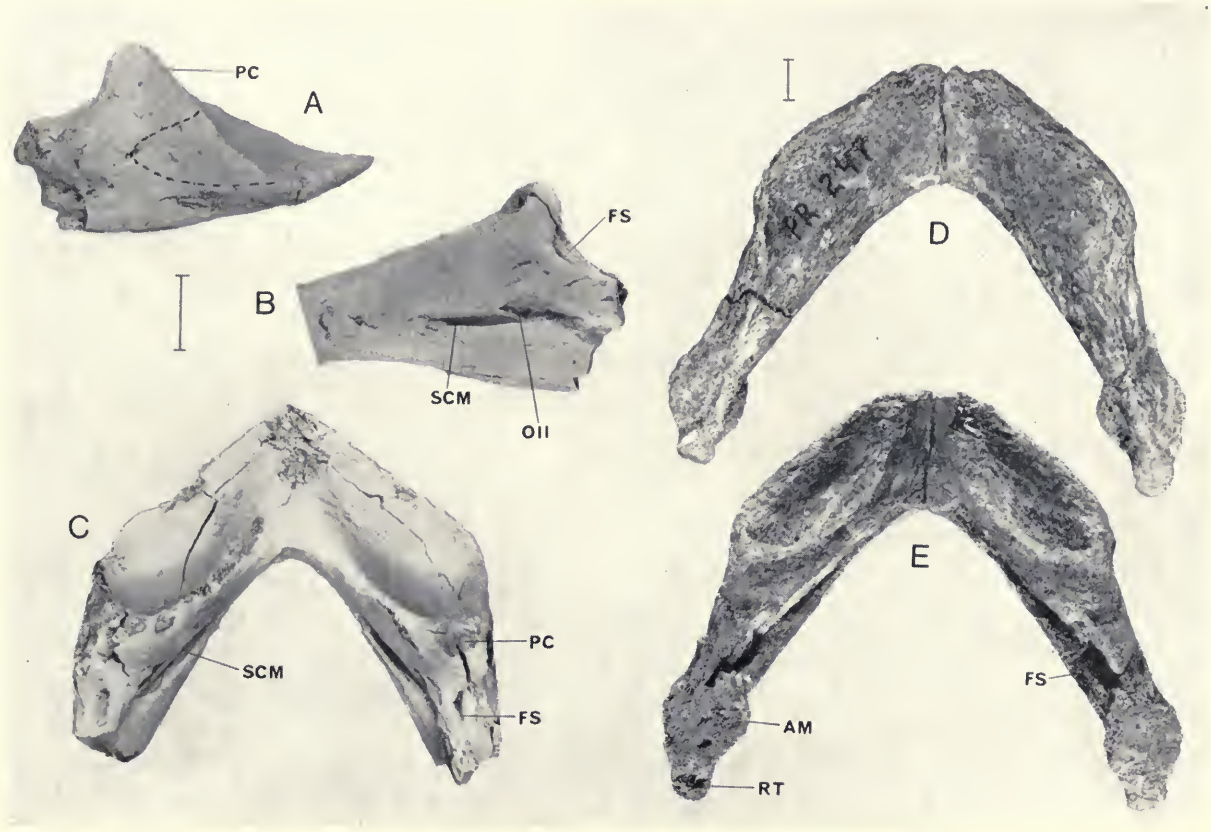
The inner face of each ramus (Fig. 22B) exposes the *fossa meckelii* and the *sulcus cartilaginis meckelii*. Dorsally the *fossa* is poorly preserved and plastered up, but more ventrally, the *sulcus cartilaginis meckelii* can be seen extending anteriorly. The foramen for the inferior maxillary nerve, or the *ostium inferius inframaxillaris* of Ogushi (1911), is present just above the ventral border of the fossa.

The jaw is 54 mm. wide at the coronoid processes while the Selma specimen is 105 mm. wide at that point.

B. barberi

This specimen (Fig. 22D, E) agrees for the most part with *B. cooki*, but the posterior parts are preserved and some (but not all) of the sutures may be seen. Most of the bone is weathered and eroded.

FIG. 22. A, B, C, *Bothremys cooki* (type). D, E, *Bothremys barberi* (FMNH PR 247). A, lateral - dotted lines indicate extent of pit. B, medial. C, dorsal. D, ventral. E, dorsal. Scale - 1 cm. Abbreviations on page 236.


A
PC
B
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The dentaries agree with *B. cooki,* but the symphysis lacks the thickened posterior edge. The pits are relatively smaller (only slightly) and the bone is thicker in the Selma jaw. This may be due to the larger size of this specimen (about twice the size of *B. cooki.*)

What appears to be a suture defining the coronoid may be followed on the left ramus and partially on the right. Dorsally it is behind the coronoid process, about one-third of the distance between that and the articulation. It proceeds down the lateral side slanting anteriorly until it is about halfway down the jaw. There it seems to split into two sutures, one going ventrally, the other curving anteriorly. The anterior one (the coronoid) goes into the pit and bisects the structure at least partially. It continues out the medial edge of the pit, slanting dorsally. On the medial surface of the jaw this suture makes a wide ventral curve, bordering the dorsal part of the *fossa meckelii,* then curving dorsad to just behind the coronoid process. The coronoid, then forms the upper half of the conical pit. This contrasts with the coronoid of living pelomedusids in which it extends only slightly, if at all, onto the triturating surface.

The dentary has a long ventral process that extends posteriorly as in living pelomedusids.

The medial border of the *fossa meckelii* is broken. It is the same as in *B. cooki* except that here the dorsal limits are exposed. The shape is quite similar as in the living genera. The antero-posterior length of the fossa is greater than in *Chisternon hebraicum* (AMNH 5904). The position of the *ostium inferius canalis inframaxillaris* is very similar in *Bothremys* and *Chisternon* as well as in the living pelomedusids. As in *B. cooki,* the *sulcus cartilaginis meckelii* extends to just behind the symphysis.

The *area articularis mandibularis* forms the posterior border of the *fossa meckelii.* The overall shape of the *area articularis* is most similar to *Podocnemis madagascariensis.* The surface is slightly convex and nearly circular in outline. Most other pelomedusids have strongly convex surfaces. A retroarticular process, slightly longer than the one in *P. madagascariensis* extends posteriorly from the *area articularis mandibularis.*

A small portion of the right squamosal as well as parts of the exoccipitals are preserved in *B. barberi,* but they are too fragmentary and crushed to describe.

RELATIONSHIPS

The skull of *Bothremys* possesses the following characteristics which demonstrate that the genus is a member of the Suborder Pleurodira as currently defined (Romer, 1956):

1) Frontal enters orbital margin (also in *Chelonia mydas* and *Corsochelys haliniches*, Zangerl, 1960; p. 287; see also Simpson, 1938);
2) prefrontal lacks descending process to vomer;
3) quadrate closed behind stapes;
4) articular surface on mandible slightly convex.

The following shell characters support this assignment:

1) fusion of ilia to carapace and fusion of pubes and ischia to plastron;
2) presence of lateral mesoplastra.

The two families of pleurodires universally recognized are the Pelomedusidae and the Chelyidae (Zangerl, 1948; Romer, 1956). The skull of *Bothremys* has the following pelomedusid characters which are lacking in chelyids:

1) prefrontals large and in sagittal contact for all their length;
2) nasals absent;
3) lower jaw with broad triturating surfaces.

The presence in *Bothremys* of a vomer, however, is a chelyid character. A vomer also exists in *Podocnemis vogli*, an otherwise acceptable pelomedusid. This fact together with the inference that animals not far removed from the chelyid-pelomedusid split might all retain vomeres, tends to lessen the strength of this character. The lateral mesoplastra of the genus *Bothremys* are also diagnostic of pelomedusids.

Relationships beneath the family level are more difficult to determine. Zangerl (1948, pp. 39-52) has shown that the shell of *"Podocnemis alabamae"* (*Bothremys barberi*) is most similar to the shell of the living South American species of *Podocnemis*, and he suggested that *"P. alabamae"* was a good morphologic ancestor to them. The skull, on the other hand, was considered to be quite distinct from the living genera as early as 1891 when Bauer (1891, p. 423) erected the family Bothremydidae based on this genus. Putting aside for the present the possibility of its being placed in a separate family, the jugal specializations of *Bothremys* (see descriptive

section) remove it from the direct ancestry of any pleurodires in which the skull is known.

Some positive statements, however, can be made about more general relationships. The posterior position of the quadrate and the well-developed vomer are found together only in *Bothremys*. This suggests that *Bothremys* may be closer to the ancestral pelomedusid condition than are the other pelomedusid genera. This is a very shaky supposition, but it may be strengthened by examining the pelomedusids known by skulls. *Podocnemis* (Siebenrock, 1897) and *Dacquemys* (Williams, 1954a) have an enlarged "carotid canal," a feature which is "advanced" for pleurodires (see Williams, 1954a). *Stereogenys* (Andrews, 1906, p. 297; Dacqué, 1912; Williams, 1954a) has an enlarged carotid opening as well as a well-developed secondary palate. The areas in question are not preserved in *Shweboemys* (Swinton, 1939). *Pelusios* and *Pelomedusa*, although having "normal" carotid canals, also have the quadrate far anterior to the occiput (as in the preceding genera: *Podocnemis*, *Pelomedusa*, *Pelusios*, *Stereogenys*, and *Dacquemys*), a condition not found in amphichelydians. *Carteremys* (Williams, 1953; Carter, 1852) has not been described in enough detail to determine the features being discussed here. Therefore, although *Bothremys* is highly specialized in the structure of the cheek and triturating surfaces, it is more primitive than known pelomedusids in its other characters:

1) presence of a vomer;
2) absence of enlarged carotid canals;
3) posterior position of quadrate.

The shell morphology of *Bothremys* may be reconciled with this information from the skull. The similarity of the shell of the South American *Podocnemis* with *Bothremys* might be due to convergence, but it more probably indicates that this is a primitive pattern among pelomedusids and was retained by *Podocnemis* (it is also found in *Roxochelys*, see Price, 1953, an upper Cretaceous pelomedusid from Brazil).

In conclusion, *Bothremys* has features, such as the presence of the jugals on the triturating surfaces (not found in any other known chelonian), that indicate considerable divergence from what would be considered a "generalized condition." However, other evidence from the skull and shell suggests that *Bothremys* represented a lower level of organization within the pelomedusids than has been recognized in other pelomedusid genera.

THE ADAPTATIONS OF *BOTHREMYS*

The function of the large palatal and mandibular pits in *Bothremys* has been commented on by earlier authors. Leidy (1865, p. 111) wrote, "The function of the latter (the pit) . . . is difficult to comprehend. It does not appear to be an alveolus for a tooth; but probably it may have accommodated a corneous tooth-like process springing from a corresponding hollow of the lower jaw." Baur (1891, pp. 423–424) suggested the presence of "a large tusk" in the pits. Hay (1908, p. 104) believed that the tooth idea was improbable and made another suggestion: "The whole construction of the skull of *Bothremys* indicates that it was accustomed to crush hard objects as food. Probably these objects were of such a nature that economy of force demanded that they should be brought to a particular spot on the jaw for crushing. To provide for the rapid reproduction of the horn beneath these areas for crushing, these pits became developt in a way analogous to the human 'nailbed.' "

Before discussing the merits of these ideas, the morphology of the structures involved should be summarized. There are two pits in the palate, principally formed by the jugals, but all of the surrounding bones including the cheek are modified to form the pits. Each pit is thickest (see cross-section) about midway in the cone. The triturating surfaces occupy most of the palate and have an overall form of two funnels opening ventrally. The lower jaws have matching structures which, however, do not open directly upward into the jugal pits, but open dorso-anteriorly.

Hay was almost certainly right in thinking that *Bothremys* was toothless. The "corneous tooth-like process" of Leidy has a somewhat greater possibility; however, the horny covering of recent turtles rarely forms a structure that is not present in the underlying bone. Thicknesses vary, but whole structures, like a large tusk, are not known to occur independent of an osseous core. Therefore, it seems likely that the whole triturating surface was covered by horny material, thickest in the tips of the pits but not forming tusk-like structures.

This inference is most like the suggestion of Hay previously quoted. However, Hay also thought that the pits were areas of rapid horn production and were not expressed on the external surface. It would be difficult to disprove this, but it is more probable that the pits were expressed as depressions in the external horny covering as in living turtles.

If this latter suggestion were correct, the pits might function to crack hard objects, slightly larger than the pits, which otherwise would be difficult to grasp or hold onto by means of a "normal" triturating surface. Certain ovoid molluscs (gastropods?) might comprise the food of *Bothremys*. There is a disadvantage to this hypothesis since it seems to mean that a particular individual of *Bothremys* would be limited to objects of a certain size range, because larger or smaller ones could not fit the pits. The crushing function of the pits is substantiated by other structural evidence. High and well-developed coronoid processes, as in *Bothremys* (Fig. 22A,B), are characteristic of turtles with crushing habits (see Stejneger, 1944, plate 30, for an example in *Amyda*). The posterior position of the articulation and the position of the pits immediately adjacent to the coronoid processes result in an efficient crushing mechanism with the adductor musculature attached close to the object to be crushed, but far from the fulcrum.

ABBREVIATIONS

AM - area articularis mandibularis
ANE - apertura narium externa
BO - basioccipital
BS - basisphenoid
CH - region of cerebral hemispheres
CL - cavum labyrinthicum
CM - condylus mandibularis
CO - condylus occipitalis
COST - costal
CP - crista pterygoidea
CR - cartilaginous ("rider") fill of supraoccipital
CT - cavum tympani
DS - dorsum sellae
E - epiplastron
ENT - entoplastron
EO - exoccipital
F - frontal
FAC - foramen anterius canalis carotici interni
FCI - foramen posterius canalis carotici interni
FM - region of foramen magnum
FNT - foramen nervi trigemini
FPC - foramen posterius canalis carotici interni
FPP - foramen palatinum posterius
FPR - foramen praepalatinum
FRV - foramen pro ramo nervi vidiani
FS - fossa mecklii
HA - hiatus acusticus
HYO - hyoplastron
HYPO - hypoplastron
ICA - incisura columellae auris
J - jugal
LP - lateral process of parietal
M - maxilla
ME - mesoplastron
N - neural
NUC - nuchal
OII - ostium inferius canalis inframaxillaris (see Ogushi, 1911)
OP - opisthotic
P - parietal
PC - processus coronoideus
PE - peripheral
PG - pygal
PIP - processus inferior parietalis
PL - palatine
PM - premaxilla
PO - postorbital
PPE - processus pterygoideus externus
PR - prootic
PRF - prefrontal
PT - pterygoid
Q - quadrate
RBS - rostrum basisphenoidale
SCM - sulcus cartilaginis meckelii
SET - sella turcica
SF - sulcus olfactorius
SOC - supraoccipital
SPG - suprapygal
SQ - squamosal
SU - sulcus cavernosus
V - vomer
X - xiphiplastron

INSTITUTIONS:

AMNH - American Museum of Natural History
ANSP - Academy of Natural Sciences of Philadelphia
FMNH - Field Museum of Natural History

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